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DIFFERENT MODES OF EVOLUTION AND ADAPTIVE RADIATION IN THE POMATIOPSIDAE (PROSOBRANCHIA: MESOGASTROPODA)

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ABSTRACT

Two subfamilies of the Pomatiopsidae are shown to have different tempos and modes of evolution. Data for the Triculinae are not new but represent a synthesis of several data sets (Davis, 1979, 1980; Davis & Greer, 1980). Data for the Pomatiopsinae with emphasis on the *Tomichia* radiation of South Africa are new. The distribution of modern pomatiopsid taxa is vicariant, a relict distribution with a secondary elaboration in Southeast Asia and the Far East extending to North America. There are eight pomatiopsine genera, one each in South Africa, South America, and Australia; one genus is found in an arc from western China to the Philippines and Sulawesi with taxa reaching Japan; two are endemic in Japan; one is found in Manchuria, Japan, and western U.S.A.; one is endemic in the U.S.A. There are 16 triculine genera, all but one of which are located entirely in Southeast Asia or western China. *Tricula* extends in an arc from India through China to the Philippines and in an arc through Burma to Malaysia.

The Triculinae have undergone an extraordinary endemic radiation in the Mekong River, yielding three tribes, 11 genera and over 90 species in a period of about 12 million years. This burst of cladogenesis was apparently driven by extrinsic processes correlated with the massive tectonics caused by the Himalayan orogeny that led to the formation of the major river systems of Southeast Asia, and western China. The morphological changes in the entirely aquatic group of snails that marked the entrance into various new adaptive zones involved a series of innovations in the female reproductive system, the male reproductive system posterior to the penis, and the central tooth of the radula. Bursts of speciation following each morphological innovation or series of correlated innovations yielded clusters of species that are considered discrete genera. The genera are separated by distinct gaps defined by morphological distances that are measures of morphological changes indicative of entrances into new adaptive zones.

Pomatiopsine taxa are aquatic, amphibious, or terrestrial. Modes of evolution in the Pomatiopsinae of the southern continents are in marked contrast to those in the Triculinae. In South Africa there are, at most, eight species of *Tomichia* with an evolutionary history of at least 80 million years. In Australia there are, at most, nine species of *Coxiella*. *Tomichia* and *Coxiella* are very similar anatomically. No burst of cladogenesis or considerable speciation is seen. Species of *Tomichia* do not differ very much in anatomy. The apparent low rate of speciation and lack of cladogenesis correlate with the lack of tectonic upheaval and gradual climatic changes since proto-*Tomichia* and proto-*Coxiella* were separated by the breakup of Gondwanaland. The limited *Tomichia* radiation is apparently in response to increasing aridity spreading from west to east in South Africa since the breakup of Gondwanaland. Speciation has not involved morphological modification but rather, adaptation to different ecological settings: freshwater streams, freshwater lakes, amphibious ecotones, temporary brackish water pools. Preadapted morphological features for an amphibious existence were probably the large, powerful foot and the elongate spermathecal duct.

The tempo of the Mekong River triculine evolution is rapid (R = about 0.40 contrasted with a slower rate (R = about 0.139) for the *Tomichia* radiation. The mode of triculine evolution is rapid, episodic speciation involving considerable morphological innovation and cladogenesis, all associated with extreme tectonism. The mode of *Tomichia* evolution involves a physiological radiation with low morphological diversity associated with gradual climatic change and general absence of tectonism.

INTRODUCTION

Modes and tempos of evolution above the species level are highly relevant topics for contemporary students of biological evolution. In considering tempos I am concerned with rates of cladogenesis, the number and extent of adaptive radiations in phyletically allied clades (per unit time), and the rate of extinction of species and lineages. By extent of

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adaptive radiation, I mean the number of species of a single radiation and the different niche dimensions these species occupy.

In considering modes of evolution, I am concerned with how organisms respond to the selective pressures of different types of changing environments, and with how organisms respond to different rates of environmental change. The presumption is made that speciation and evolution above the species level will not occur in environmental stasis.

The purpose of this paper is to demonstrate two vastly different modes and tempos of evolution in the rissoacean family Pomatiopsidae. One mode involves a radiation of considerable morphological uniformity but physiological divergence in a setting of gradual environmental change. The other mode involves a radiation exhibiting numerous morphological innovations associated with rapid tectonic environmental changes. The most important comparisons made here involve the extraordinary triculine radiation in the Mekong River and the more modest *Tomichia* radiation in South Africa. Data pertinent for discussing the triculine radiation have been published (Davis, 1979, 1980; Davis & Greer, 1980). Data for the *Tomichia* radiation are new. Two different clades are involved, because the Mekong River radiation belongs to the Triculinae and *Tomichia* is a member of the Pomatiopsinae. Together these two subfamilies comprise the Pomatiopsidae as recently defined (Davis, 1979).

The family Pomatiopsidae

The origin and evolution of the family have been discussed with emphasis on the adaptive radiation of the Triculinae in the Mekong River (Davis, 1979). The evolutionary topology of the family is shown in Fig. 1 based on the hypothesis that the Pomatiopsidae evolved and diverged into two Gondawanian subfamilies prior to the breakup of Pangaea.

Published zoogeographical, morphological, and paleontological data (Davis, 1979) are consistent with the following concepts: 1) the distribution of modern pomatiopsid taxa is vicariant. There is a relictual distribution in the southern continents with a secondary elaboration in the Far East extending to North America (Table 1). 2) Triculinae and Pomatiopsinae were introduced into the Asian mainland via the Indian Plate. 3) The patterns of distribution of Pomatiopsidae throughout Asia and North America and the direction of evolution of derived morphological character states indicate a direction of evolution from Gondawanaland to Asia (Davis, 1979).

The subfamily Triculinae

The subtending of the Asian continent by India initiated the Himalayan orogeny beginning in the Oligocene some 38 million years ago (Molnar & Tapponier, 1975). The orogeny began at the western end of the mountain chain and spread eastward as the Indian Plate rotated, bringing the northeast corner into contact with the Asian mainland in the Miocene. As the Tibetan region was lifted from the sea, drainage patterns were initiated that became the major rivers of Southeast Asia and much of China. These are the Irrawaddy, Salween, Mekong, and Yangtze rivers. Estuarine and finally fluviatile deposits were laid down in northern Burma at the end of the Miocene; in the Pliocene the sediments of the Irrawaddy River became entirely freshwater (Pascoe, 1950).

It is apparent that proto-Triculinae were introduced from the Indian Plate into the newly forming drainages of the Asian mainland (Davis, 1979, 1980; Davis & Greer, 1980). All Triculinae thus far studied are entirely freshwater in streams, lakes, and rivers. They extend in three arcs. One arc extends from northwestern India through China to the Philippines. The second arc extends from India through northern Burma and western Yunnan, China and throughout the Mekong River drainage but ending in northern Cambodia. The third arc extends through northern Burma, northwestern Thailand into Malaysia.

Tricula, the genus with the most generalized morphology and least derived character states (Davis & Greer, 1980) is found along each of these arcs. Taxa with the most derived character states are found endemic in the Mekong and Yangtze River drainages and in lakes in Yunnan, China between the rivers (Davis, 1980; Davis & Greer, 1980). These derived taxa are *Halewisia* and *Pachydrobia* of the Triculini and all members of the Lacunopsini and Jullieniini. As shown in Table 1, of 16 genera and 120 species of Triculinae, 10 genera and 92 species (76.7%) are endemic to the Mekong River drainage.

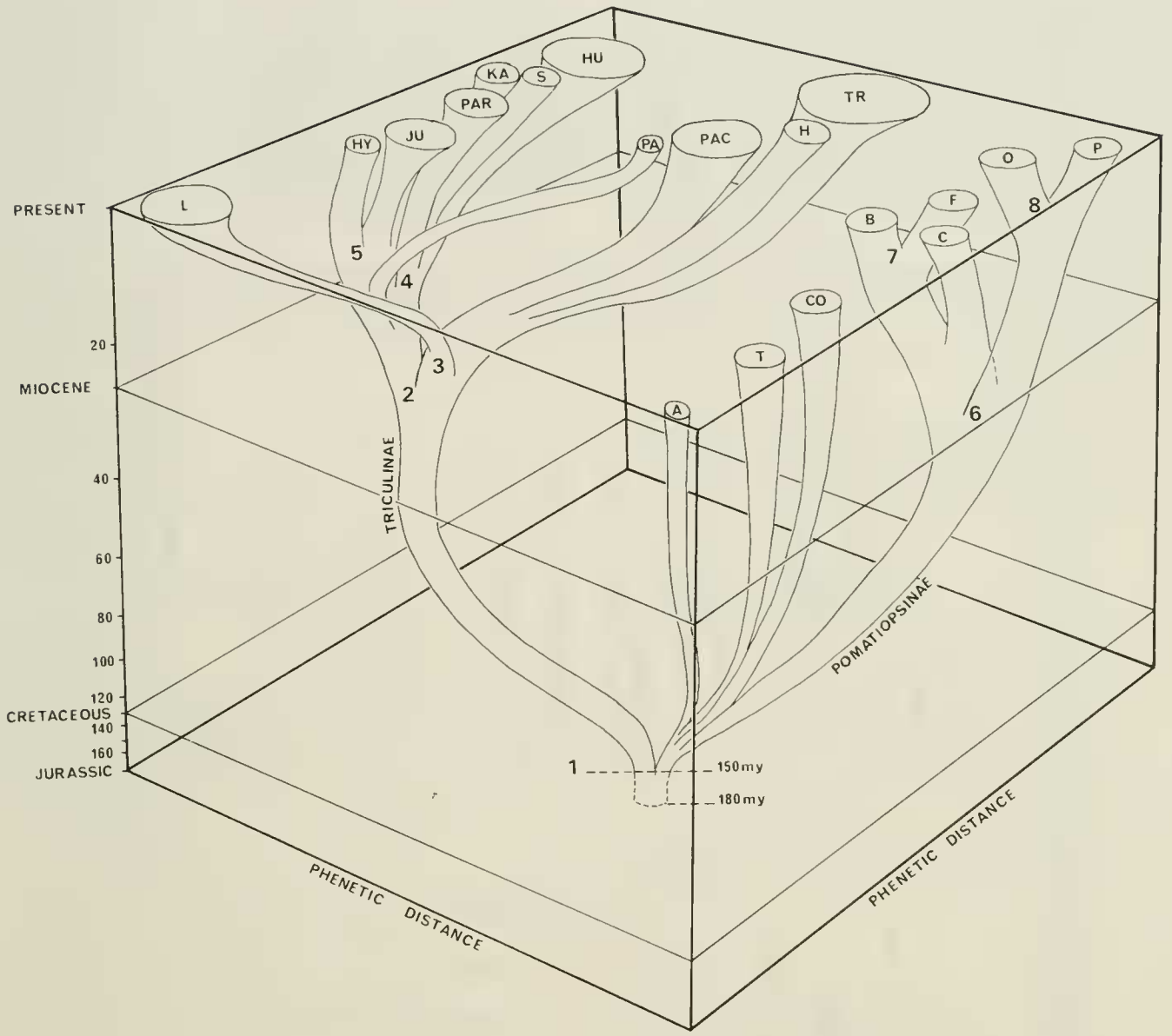


FIG. 1. Phyletic topology of the Pomatiopsidae with time given in millions of years (on a log scale) from the Jurassic to the present. Branching points: 1. Triculine and pomatiopsine lineages established in Gondwanaland prior to the breakup of the southern continent. 2. Divergence to form the Jullieniini (left grouping) in the Miocene. 3. Radiation of specialized *Lacunopsis* (Lacunopsini), which diverges from the Triculini. *Lacunopsis*, on shell characters, resembles marine and freshwater Neritidae. Some species converge on *Anculosa* (Pleuroceridae), *Littorina* (Littorinidae), or *Calyptraea* (Calyptraeidae). 4. Seven genera evolved in the Miocene, probably much at the same time. *Pachydrobiella* (PA) converges on *Pachydrobia* (PAC) of the Triculini in shell shape and structure. 5. Anatomical and shell data clearly indicate that *Hydrorissoia* (HY) and *Jullienia* (JU) diverged from a common ancestor. 6. A late Miocene radiation took place in Japan, giving rise to the endemic genera *Blanfordia* (B) and *Fukuia* (F), and *Cecina* (C). *Cecina* spread to western North America, while *Pomatiopsis* (P) occurs only in the U.S.A. 7. *Blanfordia* and *Fukuia* have either diverged from a common ancestor or are the same genus. Data thus far available support the former interpretation.

A. *Aquidauania*, South America. B. *Blanfordia*, Japan. C. *Cecina*, Japan, Manchuria, U.S.A. CO. *Coxiella*, Australia. F. *Fukuia*, Japan. H. *Halewisia*, Mekong River. HU. *Hubendickia*, Mekong River. HY. *Hydrorissoia*, Mekong River. JU. *Jullienia*, Mekong River. KA. *Karelainia*, Mekong River. L. *Lacunopsis*, Mekong River. O. *Oncomelania*, China, Japan, Philippines, Sulawesi. P. *Pomatiopsis*, U.S.A. PA. *Pachydrobiella*, Mekong River. PAC. *Pachydrobia*, Mekong River, PAR. *Paraprosothenia*, China. Mekong River (Thailand, Lao). S. *Saduniella*, Mekong River. T. *Tomichia*, South Africa. TR. *Tricula*, India, Burma, China, Philippines, Mekong River (from Davis, 1979).

TABLE 1. Classification, numbers of taxa, and zoogeography of the Pomatiopsidae. ( ), number of species; M, endemic in Mekong River drainage; +, placement of *Delavaya* (1), *Fenouilia* (1), and *Parapyrgula* (1) uncertain; they are probably Jullieniini.

Pomatiopsinae			Triculinae		
Aquidauania Davis, 1979	(1)	South America	Tribe Triculini +		
Blanfordia A. Adams, 1863	(2)	Japan	*Halewisia* Davis, 1979	(2)	Thailand, Laos, Cambodia: M
Cecina A. Adams, 1861	(1)	Japan, Manchuria, northwest United States	*Pachydrobia* Crosse & Fischer, 1876	(17)	Thailand, Laos, Cambodia: M
Coxiella E. A. Smith, 1894	(10)	Australia, Tasmania	*Robertsiella* Davis and Greer, 1980	(2)	Malaysia
Fukuia Abbott & Hunter, 1949	(2)	Japan	*Tricula* Benson, 1843	(20)	India, China, S.E. Asia
Oncomelania Gredler, 1881	(2)*	China, Japan, Taiwan, Phil., Sulawesi	Tribe Lacunopsini		
Pomatiopsis Tryon, 1862	(4)	United States	*Lacunopsis* Deshayes, 1876	(15)	Thailand, Laos, Cambodia: M
Tomichia Benson, 1851	(7)	South Africa	Tribe Jullieniini		
			Hubendickia Brandt, 1968	(16)	Thailand, Laos, Cambodia: M
			Hydrorissoia Bavay, 1895	(9)	Thailand, Laos, Cambodia: M
			Jullienia Crosse & Fischer, 1876	(16)	Thailand, Laos, Cambodia: M
			Karelainia Davis, 1979	(4)	Thailand, Laos, Cambodia: M
			Lithoglyphopsis Thiele, 1928	(4)	China
			Pachydrobiella Thiele, 1918	(1)	Thailand, Laos, Cambodia: M
			Paraprososthenia Annandale, 1919	(10)	Thailand, Laos, Cambodia: M
			Saduniella Brandt, 1970	(1)	Thailand, Laos, Cambodia: M
TOTAL: 8 genera	29 species		16 genera	120 species (92 endemic in the Mekong River)	

*O. *hupensis* has 6 subspecies.

The tribes and genera of the Triculinae are separated by discrete qualitative morphological gaps (Davis, 1979, 1980; Davis & Greer, 1980). Some 28 characters are of use in recognizing these taxa because the taxa have shared derived states of these characters and/or uniqueness of certain derived states (Table 2). Of these characters, 14 are from the female reproductive system (50%), seven are from the male reproductive system (25%) (only one is from the penis), four are shell characters (14%), two are radular characters (7%), and one is osphradial (4%).

The Triculinae provide an excellent opportunity for studying how higher taxa evolve. The monophyletic assemblage (Davis, 1979) is large enough to explore how species of various adaptive zones have radiated, and to un-

TABLE 2. A list of 28 characters that are used to recognize tribes and genera of the Triculinae. References to illustrations or discussions of character-states are given; these are one or more of Davis, 1979, 1980 (= 1980a below); Davis & Greer, 1980 (= 1980b below); Davis et al., 1976.

Shell	
1. shape	1979, figs. 28–30; 1980a, fig. 7
2. sculpture	1979, figs. 28–30; Table 12; 1980a, fig. 7
3. size	1979, figs. 28–30; Table 11; 1980a, fig. 7; Table 6
4. thickness	1979, figs. 28–30; 1980a, fig. 7
Central tooth	
5. anterior cusp morphology	1979, fig. 4; 1980a, fig. 6
6. size of blade supports	1979, fig. 4; 1980a, fig. 6
Osphradium	
7. length	1976, fig. 7
Female reproductive system	
8. gonad morphology	1979, figs. 11–15; 1980a, fig. 11
9. coiling of the oviduct posterior to the bursa copulatrix	1980a, figs. 4, 8, 13
10. position of the opening of the seminal receptacle	1979, figs. 3, 11–18; 1980b, fig. 10
11. length of seminal receptacle	1979, fig. 12
12. oviduct configuration at the bursa copulatric region	1979, fig. 3
13. length of the bursa copulatrix relative to length of pallial oviduct	1979, figs. 12, 13
14. length of duct of the bursa copulatrix	1979, figs. 11–16; 1980a, fig. 13
15. position of the pallial oviduct relative to the columellar muscle.	1979: 107
16. Coiling of the spermathecal duct	1979, fig. 12
17. encapsulation of the spermathecal duct	1980b, fig. 7
18. vestibule of the spermathecal duct	1980b, fig. 7
19. extension of the spermathecal duct into the mantle cavity (= sperm uptake organ)	1979, fig. 14C; 1980b, fig. 10
20. position of opening of the spermathecal duct into the bursa copulatrix complex of organs	1979, fig. 3; 1980a, figs. 8, 13; 1980b, fig. 10
21. method by which sperm enter female reproductive system at the posterior end of the mantle cavity	1979, fig. 3; 1980a, figs. 5, 8; 1980b, fig. 10
Male reproductive system	
22. gonad morphology	1979, fig. 19; 1980a, fig. 11; 1980b, fig. 9
23. position of coiling of the seminal vesicle	1979, figs. 11–15; 1980a, fig. 12
24. relative length of the vas deferens (Vd^a) between the gonad and seminal vesicle	1980a, fig. 12
25. coiling of the vas deferens posterior to the penis	1979, fig. 12A
26. position where vas deferens leaves the prostate	1979, figs. 14, 15
27. penis has stylet or papilla	1976, fig. 10; 1979, fig. 10; 1980b, fig. 9
28. status of vas efferens	1979, figs. 11–15; 1980a, fig. 11; 1980b, fig. 9

derstand the directions of morphological change that permitted the crossing of thresholds of various adaptive zones to new adaptive zones.

In the Triculinae, as in other higher taxa, we see four aspects of adaptive radiation: first order adaptive radiations, null radiation, second order adaptive radiations, and macro-adaptive radiation.

The term adaptive radiation was first used by Osborn (1918) and fully exploited by Simpson (1949) who stated: "Adaptive radiation is, descriptively, this often extreme diversification of a group [e.g. mammalian or reptilian radiation] as it evolves in all the different directions permitted by its own potentialities and by the environments it encounters." Stanley (1979) stated: "Adaptive radiation is the rapid proliferation of new taxa from a single ancestral group." These authors are discussing what I call here macro-adaptive radiation, a higher taxon or a higher taxon clade that is, in fact, recognized as such because of its component clades. The Triculinae are a macro-adaptive radiation.

A first order radiation is equated with a genus, which is a composite of at least two, but usually more than two species. The entrance into a new adaptive zone made possible by a new morphological or physiological innovation is associated with the rapid proliferation of new species that fill various niche dimensions. A null radiation is a monotypic genus, a taxon recognized by the discrete morphological gap from other genera to which it is phyletically allied. Such a genus may be the basis for a first order radiation of the future, or represent a dead-end due to the very nature of the morphological innovation(s) that distinguishes it. Planispiral *Saduniella* of the Triculinae is such a genus. A second order radiation involves two or more phyletically allied first order radiations and can be equated to named taxa between generic and high taxon clades under discussion. Within the Triculinae, the tribes Triculini and Jullieniini are second order radiations.

Detailed discussions of the evolution of derived character-states and taxa with those states have been given (Davis, 1979, 1980; Davis & Greer, 1980). In review, the most profound changes involved the reproductive systems as the progenitors of the modern Triculinae adapted to the evolving Mekong and Yangtze River systems. Changes were essentially in two directions involving two clades, the Lacunopsini and Jullieniini. These changes show divergence from *Tricula,* which

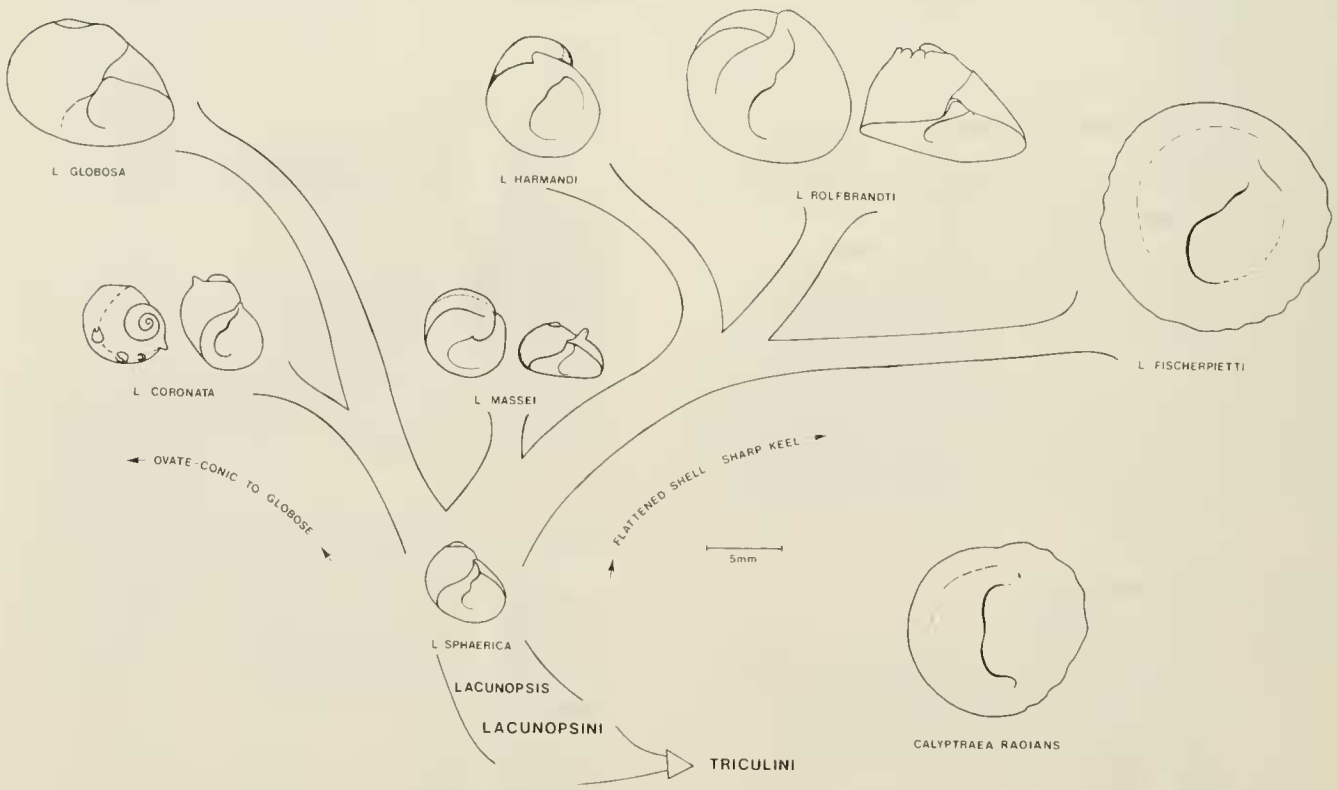


FIG. 2. Shells of representative species of the Lacunopsini showing diversity in shell shape and showing a closer relationship of the Lacunopsini to the Triculini than to the Jullieniini (also see Fig. 1). The marine mesogastropod *Calyptraea radians* is illustrated to show how similar the species is to *L. fischerpietti.* These two species are highly convergent in shape, growth patterns, and sculpture (from Davis, 1979).

has the most generalized character-states. Many of these derived innovations are correlated with swift-water habitats as has been shown statistically (Davis, 1979). There is a lack of species with generalized character-states adapted to swift-water habitats.

The Lacunopsini (Fig. 2) most likely evolved from an ancestor that also gave rise to *Tricula bollingi* (Davis & Greer, 1980). A single first order radiation is involved, all in the Mekong River. The niche dimensions filled are swift-water habitats on rocks where species differences are seen in shell shape and sculpture, and positional relationships in the water column involving rock slope, depth, rock surface, degree of current. Shell shapes are astonishing for freshwater hydrobioids as shapes converge on those of marine Neritidae, Littorinidae, and Fossaridae. The most remarkable changes in the reproductive system are the loss of the seminal receptacle as seen in *Tricula* and the development of several accessory seminal receptacles, and the degree to which the pericardium is modified and used to accommodate sperm during reproduction. All species are similar in that the central tooth is a derived type (Fig. 5) modified for scraping food from rock.

The Jullieniini (Fig. 4) comprise one of the most spectacular second order molluscan radiations ever seen in freshwater. This radiation in the Mekong River has five first order radiations and two null radiations. We know too little about the Chinese genera *Litho-*

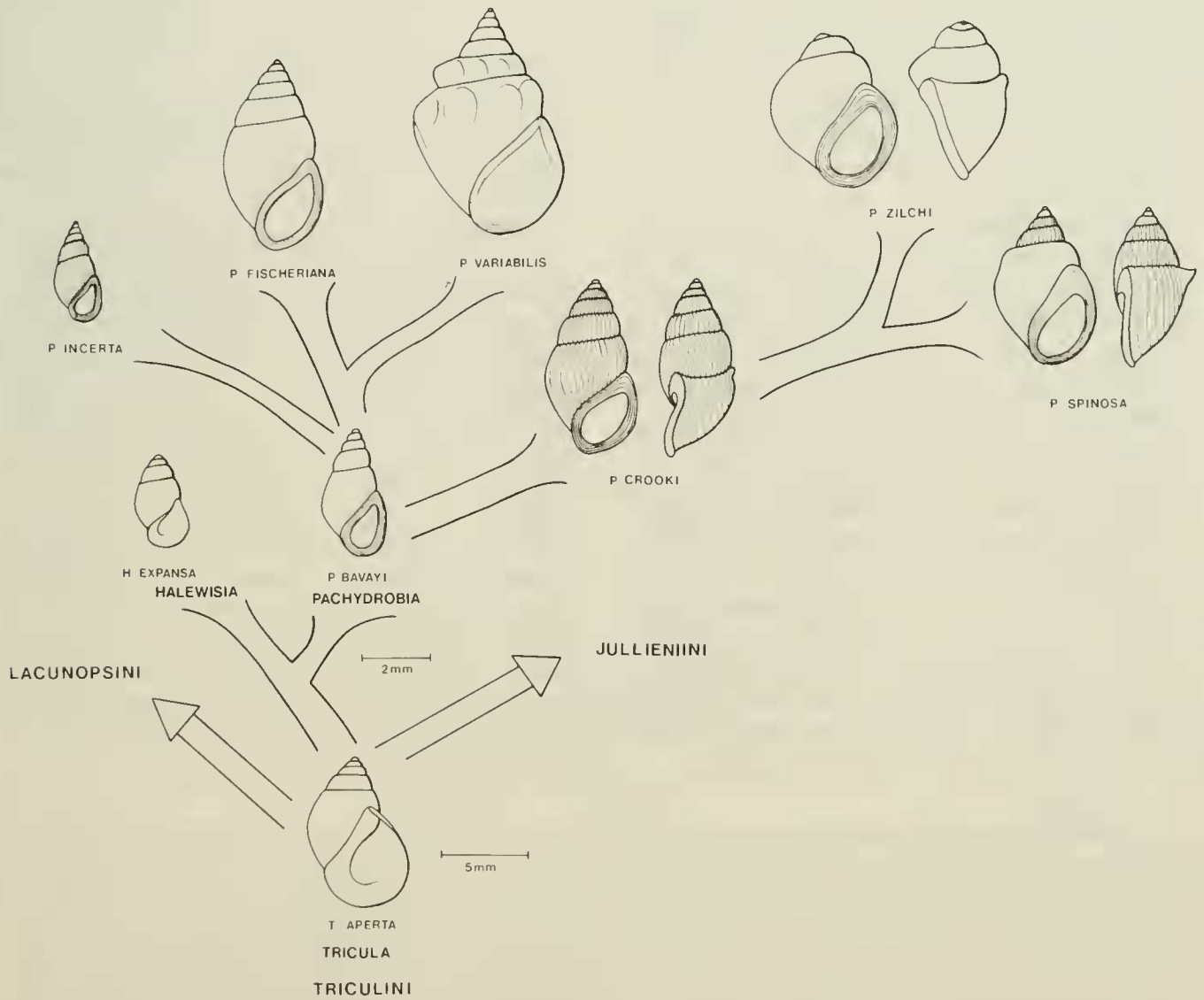


FIG. 3. Shells of representative species of the three genera of the Triculini. The implication of this tree-like configuration is that *Pachydrobia* has more derived character states than does *Tricula,* reflected in certain shell features, e.g. ribs, bosses (odd lump[s] on the shell), and solitary spines. Also implied is the basal status of *Tricula* relative to the divergent tribes Lacunopsini and Jullieniini, which have more derived character states (also see Fig. 1). Note also the increase in size (only *L. aperta* is drawn at a larger scale, as indicated by the 5 mm scale bar) in *P. variabilis, P. fischeriana,* etc., compared with *Halewisia* and *Tricula* (from Davis, 1979).

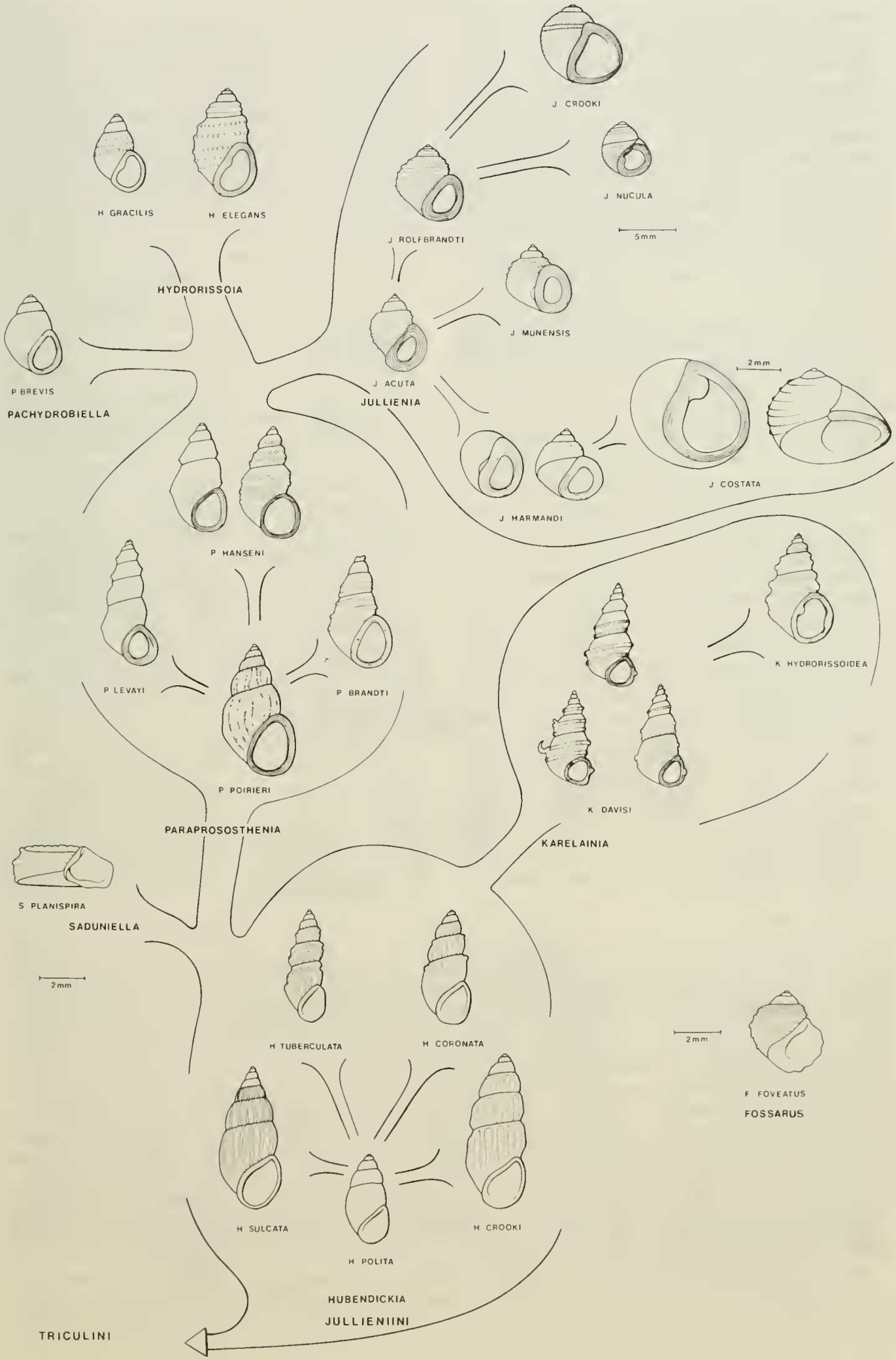
glyphopsis, Delavaya, Fenouilia, and *Parapyrgula* (Table 1) to say anything about them. Incremental derived changes in the female reproductive system are in the direction of increasing volume and complexity of the reproductive organs (Davis, 1979, 1980). The generalized hydrobioid oviduct is thrown into a 360° complex with the seminal receptacle and spermathecal duct (Fig. 6). This 360° loop is small in diameter in the least derived genus (*Karelainia*) and increases markedly in diameter in the more derived genera. The gonad is the generalized pomatiopsid type in *Karelainia* and is considerably modified in morphology in the more derived genera. Elongation of the seminal receptacle is seen in only a few species of *Hubendickia* while extreme elongation is seen in more derived genera such as *Paraprososthenia, Jullienia, Hydrorissoia,* and *Pachydrobiella.* Extreme elongation and recurving or coiling of various sections of the vas deferens are seen in the more derived genera and especially pronounced in the most derived genera, *Jullienia* and *Hydrorissoia.*

Increasing complexity in the reproductive system is associated with exploitation of differing (even if slight) reproductive strategies. Increasing bulk and complexity of the reproductive system are associated with the Mekong River triculine fauna (Davis, 1979). These species are colonizers and opportunistic species in a river that goes through an annual cycle of rampaging floods during the monsoon season (June through November) to relative quiet and shallow flow during the dry season (December through May). The floods bring high density-independent mortality because of the distribution of habitats and the sweeping away of snails from low-water depositional areas. There are high reproductive rates in the single short low-water breeding season available to these annual species. The relative volume of reproductive organs discussed above coupled with the tremendous biomass of young produced (see Davis, 1979) attest to comparatively great amount of energy put toward reproduction (contrast Pomatiopsinae, Davis, 1979: 69).

Growth and reproductive activities of Mekong River species are remarkably in phase with the annual river cycles. Different groups of species mature, reproduce, and die at different times once the dry season begins and water levels begin to drop. All Triculinae are semelparous as far as is known. Once *Pachydrobia* reproduces, the reproductive system slowly disintegrates. This is first seen in the male where the penis begins to disintegrate; it is later seen in the female where the ovary and pallial oviduct disintegrate. The snails live on for a month or more after the onset of this disintegration process. Once *Tricula aperta* has laid its eggs, it dies and there is a period of about one month when no adults are seen and no hatched young can be found.

Additionally, there is a temporal division of river habitat as regards maturation and reproduction. A given habitat may have one group of species at one period of low water that reproduce and die, to be replaced by different species that hatch, grow to maturity, etc. (Davis, 1979). The temporal division keeps pace with the annual cycle of habitat emergence. As water levels begin to decrease in October, habitats begin to emerge and form. First island masses and the larger waterfalls appear, followed by smaller islands, embayments between islands, lakes and pools on islands, smaller rapids, sandbars, and finally shallow quiet areas allowing for considerable mud deposition. From mid-October or November through June most habitats are free

FIG. 4. Shells of representative species of the seven genera of the Jullieniini grouped to reflect relationships and a radiation of shell types within each genus. The trend from bottom to top is one of generalized to specialized both in shell features and anatomy. Spiral and nodulate sculpture is derived. *Jullienia* is most specialized in terms of sculptural patterns, large size, and odd shapes (e.g. flattening of the base of the shell in some species) as well as anatomy. In *Hubendickia,* the shells, depending on the species, are smooth or ribbed. Nodes are seen on the adapical ends of the ribs in two species. In *Paraprososthenia,* shells range from smoothly ribbed, with solid spiral cords, or with spiral rows of nodes. *P. hanseni* has morphs ranging from smooth, one spiral row of nodes to several spiral rows of nodes on the body whorl. *Hydrorissoia* and *Jullienia* are, on the basis of anatomy, phenetically very similar. Together with *Paraprososthenia* they form the *Jullienia* complex. *Karelainia* parallels *Paraprososthenia* in shape and sculpture but diverges considerably in anatomy. Note that *K. davisi* has several morphs. *Fossarus foveatus* is shown as an example of convergence between unrelated taxa. *F. foveatus* is similar to species of *Jullienia* in shell shape and sculpture. *F. foveatus* is in the marine family Fossaridae. All shells are drawn to the same scale except the six *Jullienia* with the 5 mm scale bar (from Davis, 1979).


J CROOKI
J NUCULA
5mm
H GRACILIS
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J MUNENSIS
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J ACUTA
JULLIENIA
2mm
J COSTATA
J HARMANDI
P HANSENI
P LEVAYI
P BRANDTI
P POIRIERI
PARAPROSOSTHENIA
K HYDRORISSOIDEA
K DAVISI
KARELAINIA
S PLANISPIRA
SADUNIELLA
2mm
H TUBERCULATA
H CORONATA
2mm
F FOVEATUS
FOSSARUS
H SULCATA
H CROOKI
H POLITA
HUBENDICKIA
JULLIENIINI
TRICULINI

from flooding and destruction caused by the monsoons. Because of the floods, the configurations of sandbars, islands, and rapids change yearly. A population that flourished in a muddy depositional area one year may be buried under stones and cobbles the next year. Species with the most derived reproductive systems appear to grow and mature rapidly and to reproduce during lowest water. Taxa with the most generalized systems reproduce during higher water periods before and after the four-month lowest-water months (Davis, 1979).

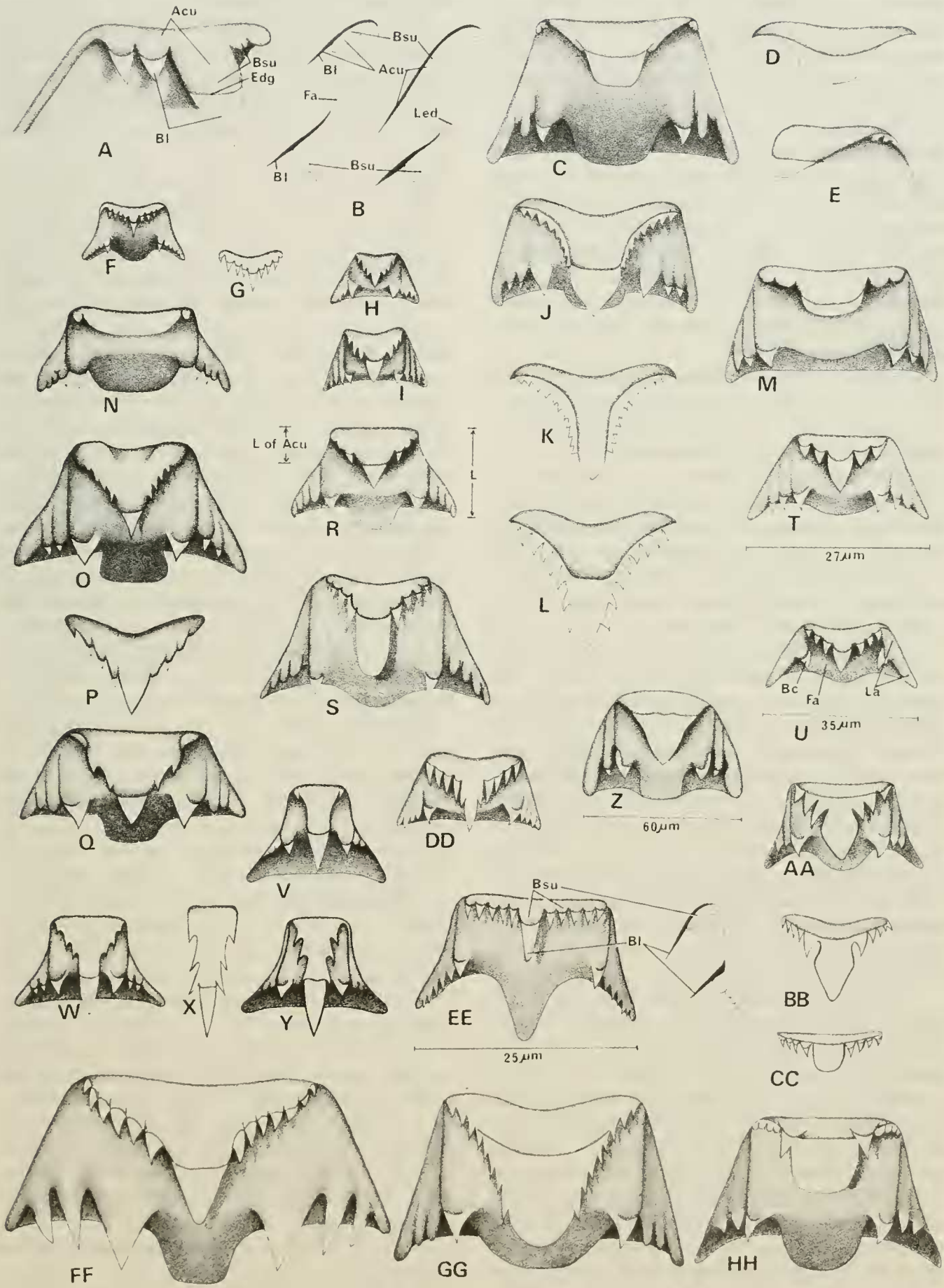
The foregoing discussion has involved 75% of the derived characters. Different feeding habits involve yet another niche dimension especially exploited in the second order Jullieniini radiation. This is reflected by the morphology of the central tooth of the radula (Fig. 5). The generalized central tooth seen in the Triculini and all Pomatiopsinae is found only in a few species of *Hubendickia* of the Jullieniini. Species of all other genera have derived types of teeth. Finally, shell characters reflect adaptations to different microhabitats and perhaps to living in sympatry with different species (Figs. 2–4). Only two or three species of *Hubendickia* have the smooth, ovate-conic, small shell that is the generalized hydrobioid type (Davis, 1980). Modification of shell characters from generalized to most derived follows a parallel course in each of the two second order and Lacunopsini first order adaptive radiations of the Triculinae. There is a net increase in size, and there appears to be a progression from smooth to ribbed, nodulate ribs, reticulate sculpture, spiral noded cords, and finally odd spines and nodes.

There is another progression from ovate-conic to diverse symmetric shapes including planispiral, and finally to asymmetry. In the Jullieniini the trends in increasing complexity of the reproductive systems generally parallel the three trends in shell characters and the trends in central tooth morphology.

It is in *Hubendickia* that we have an indication that certain sculptural character-states are related to species living in sympatry. We see a possible case of character displacement. At Khemarat, Thailand five species of *Hubendickia* live sympatrically. It is common to find four species in great numbers (hundreds) in a handful of algae. Each of these species has a distinctive shell sculpture involving ribs. One of these species was called *H. spiralis* Brandt because of pronounced spiral micro-sculpture. These species crawl over each other continuously. It seems probable, although it is untested, that sculpture serves for species recognition for mating purposes. It was determined on the basis of overall morphological similarity that *H. siamensis spiralis* was a synonym of *H. sulcata* (Bavay) of the lower Mekong River (near Cambodia) as was also *H. siamensis* Brandt of the Mun River that flows into the Mekong River at the isles of Ban Dan (Davis, 1979). No other species of *Hubendickia* lives in the Mun River where one finds the population of *H. sulcata* referred to by Brandt as *H. siamensis*. Snails of this population entirely lack spiral microsculpture. Over 100 miles south of Khemarat at Khong Island there are more than 50 species of Triculinae but few species of *Hubendickia*. Populations of *Hubendickia* are rarely sympatric in the sense that they are found

FIG. 5. Central teeth of representative species of Triculinae and Pomatiopsinae compared with the central tooth of *Hydrobia totteni*. A, B. Stylized drawings showing structures of the central tooth. Note that the blade (Bl, blackened layer) is a layer fused on the dorsal aspect of the blade support (Bsu). The lateral view of the tooth is shown in B and EE. C-E. *Hydrorissoia hospitalis* (Triculinae: Jullieniini). F, G. *Hubendickia cylindrica* (Triculinae: Jullieniini). H. *Saduniella planispira* (Triculinae: Jullieniini). I. *Paraprososthenia levayi* (Triculinae: Jullieniini). J-L. *Jullienia harmandi* (Triculinae: Jullieniini). M. *Pachydrobia variabilis* (Triculinae: Triculini). N. *Hubendickia coronata* (Triculinae: Jullieniini). O-Q. *H. gochenouri* (Triculinae: Jullieniini). R.*H. polita* (Triculinae: Jullieniini). S. *H. pellucida* (Triculinae: Jullieniini). T. *Oncomelania hupensis* (Pomatiopsidae: Pomatiopsinae). U. *Hydrobia totteni* (Hydrobiidae: Hydrobiinae). V-Y. *Hydrorissoia elegans* (Triculinae: Jullieniini). Z. *Lacunopsis conica* (Triculinae: Lacunopsini). AA-CC. *Halewisia expansa* male (Triculinae: Triculini). DD. *Karelainia davisi* (Triculinae: Jullieniini). EE. *Tricula aperta* (Triculinae: Triculini). FF. *Jullienia acuta* (Triculinae: Jullieniini). GG. *Pachydrobiella brevis* (Triculinae: Jullieniini). HH. *Halewisia expansa* female (Triculinae: Triculini) All teeth without μm bars are drawn to the same scale as EE. Z was drawn at ⅓ the magnification of EE. Note the multiserrated blade of J-L and GG and the pauciserrated blade of AA (from Davis, 1979).

Acu, anterior cusp; Bc, basal cusp; Bl, blade; Bsu, blade support; Edg, edge of the blade support; Fa, face of the tooth; L, length of tooth; La, lateral angle; L of Acu, length of anterior cusp (to the Edg); Led, lateral edge of tooth face.


Acu
Bsu
Edg
Bl
A
Bsu
Bl
Acu
Fa
Led
Bl
Bsu
B
C
D
E
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I
J
M
N
K
L of Acu
L
R
T
27 µm
O
L
P
S
Bc
Fa
La
U
35 µm
Q
DD
Z
60 µm
AA
V
W
X
Y
Bsu
Bl
EE
25 µm
BB
CC
FF
GG
HH

living intermixed on the same substrate in the same area. Spiral microsculpture is weakly developed in a few populations of *H. sulcata,* found on only some individuals of other populations, and is entirely lacking from individuals of yet other populations. It is evident that in the absence of high incidence of congeneric sympatry, spiral microsculpture breaks down.

Many shell shapes are clearly interpretable when one observes how the species live. The shells of one species converge on the shells of phyletically totally unrelated groups because the animals of these different groups position themselves on various substrates in the same way. The resemblance of various *Lacunopsis* species to marine *Littorina* has been discussed in detail elsewhere (Davis, 1979, 1980).

Tricula of the Triculini radiation (Fig. 3) has the most generalized morphology and is represented in the Mekong River by only one species, *T. aperta* (Temcharoen). The one successful Triculini radiation in the Mekong River involves *Pachydrobia.* Again, this species-rich radiation involves innovations in the female reproductive system and establishment in a range of habitat types as reflected in a range of shell morphologies that fit the trends discussed above.

It is evident that entrance into an adaptive zone, which permitted a new first order radiation of Triculinae, enabled some species of that radiation to overlap many niche dimensions of species of other first order radiations. A single scoop of a hand sieve (500 ml capacity) through a muddy substrate often yields several thousand snails of eight to ten species of three to six genera (Davis, 1979). Numerous species in sympatry on a rock or patch of mud or small area of sandy-mud is the rule, not the exception. The snails do not seem to be resource limited unless it is for space for egg deposition.

A number of species do occupy unique space. An example is *Lacunopsis fischerpietti* Brandt, the largest triculine in the Mekong River (shell diameter of 15 to 18 mm), which closely resembles the marine species *Calyptraea radians. L. fischerpietti* lives one or two per boulder on the vertical faces of huge boulders, facing the swiftest current. Other examples are: *Lacunopsis harmandi,* which lives at the interface of swiftly flowing water and air. *Jullienia costata* lives crowded by the thousands, packed shell to shell, on vertical cliff walls in rushing waterfalls, splashed continuously by the spray. Some populations of *Hubendickia polita* are nearly amphibious, living on damp rock just above the water line. *Lacunopsis massei* lives with no other species, each individual is separated by at least 15 mm from other individuals on a polished smooth horizontal rock surface over which a strong current runs and the water is at least one meter deep. Several species of *Pachydrobia* live allopatrically in sandbars where few or no other species live.

Tempo and mode of triculine evolution

Given the time period for the Himalayan orogeny, initiation of the river drainage systems involved, and the presence of freshwater sediments in the critical region of northern Burma, it is reasonable to estimate the age of the modern triculine radiation as starting about 10 to 12 million years ago at the longest (Davis, 1979, 1980). Following the arguments of Stanley (1975, 1979) I calculate R, the fractional increase of species per unit time using the equation $N_t = N_o e^{Rt}$, which is equivalent to $R = (1nN)/t$. N_o is the original number of species (= 1 considering that the Triculinae are monophyletic and a single successful introduction from the Indian Plate is all that was needed to produce the macro-radiation fanning out along the three aforementioned arcs); N is the number of species now living, t is the time, e is the base of the natural logarithm. For the Asian Triculinae as a whole $R = 0.40$ to 0.48 (My^{-1}) depending on t of 12 or 10 million years ago. This rate is extremely great and exceeds that of the mammalian Muridae that have evolved over 19 millions years ($R = 0.35$). R for the Triculinae is several times greater than for any other molluscan group known (R = about $0.067\ My^{-1}$ for several families of marine gastropods; $R = 0.046 - 0.087\ My^{-1}$ for several families of marine bivalves; see Stanley, 1979). If we calculate R for two second order radiations and major primary radiation we see the following result: Triculini, $R = 0.31\ My^{-1}$; Lacunopsini, $R = 0.23\ My^{-1}$; Jullieniini, $R = 0.35\ My^{-1}$.

This explosive monophyletic macro-radiation is coincident with the massive, abrupt, and recent tectonics of the Himalayan orogeny. The strong positive association between tectonic events, bursts of speciation and cladogenesis, endemism have been reviewed (Taylor, 1966; Davis, 1979, 1980). Rapidly shifting selective pressures and new pressures are in evidence as seen in the geological and geographically distributed aftermath of the processes forming the modern river drainage patterns of the Irrawaddy,

Salween, Mekong and Yangtze rivers. One sees in the now empty ancient river beds and dead or drying lake basins of northwestern Thailand, Laos, and northern Burma how tectonic changes created new aquatic systems only to surrender these to new stream captures, new lake formations leaving behind isolated lakes or empty basins. We see in the transient aquatic world at the eastern end of the Himalayan orogeny, over the past 12 million years, the elements needed for rapid evolutionary change, the subdivision of population into small, isolated, peripheral units (Wright, 1940). Eldredge & Gould (1972) and Gould & Eldredge (1977) argue that evolution proceeded more by rapid and episodic events of speciation in such peripheral populations than by gradual change, a theme elaborated on by Stanley (1979). We see the rapid appearance of two secondary radiations and a number of primary radiations that are separated from each other by discrete morphological gaps. Given the abundance of species that exist and the recentness of the radiation we do not see continuous series of morphological change in transition from one primary radiation to another. We do not see any semblance of gradual change. The macro-adaptive radiation of the Triculinae represents an excellent case of the punctuational model as defined by the above authors.

The problem with involving punctuated equilibrium is one of scale. How much can be resolved in the fossil record over slices of time involving one million years when new species can arise in thousands of years? Paleontologists do not have the relevant data (Smith, 1981). However, data from *Drosophila* research reviewed by Jones (1981) clearly indicate that some populations have sufficient hidden genetic variation to enable instant speciation under certain conditions, which can involve morphological and behavioral characteristics as well as reductive isolation. These conditions apparently involve organisms that disperse easily, have relatively short generation times, and live under conditions where new ecological space opens. These conditions apply to the triculine radiation and are persuasive in considering the triculines as fitting a punctuational model.

The Pomatiopsinae and the *Tomichia* radiation: Introduction

The general features of the pomatiopsine macro-adaptive radiation have been presented (Davis, 1979). There are eight genera: *Aquidauania,* Brazil, South America; *Tomichia,* South Africa; *Coxiella,* Australia; *Oncomelania,* Asia; *Blanfordia* and *Fukuia,* Japan; *Cecina,* Japan, Manchuria, western U.S.A.; *Pomatiopsis,* U.S.A. Unlike the Triculinae, various pomatiopsine taxa are amphibious, saltwater tolerant, terrestrial and arboreal in addition to being freshwater aquatic. The relictual vicariant distributions of *Tomichia, Coxiella,* and *Aquidauania* are consistent with a Gondwanaland origin, especially as these genera are more closely related to each other (in terms of overall morphological similarity) than any one of them is to the more derived *Oncomelania. Oncomelania* has a distribution from northern Burma (Pliocene-Pleistocene fossil) to Japan with an arc following the Yangtze River, through Taiwan, to the Philippines and Sulawesi (Davis, 1979, 1980).

I knew from preliminary dissections of *Tomichia ventricosa* sent to me at the University of Michigan, Ann Arbor, Michigan, U.S.A., in 1964 that this species was a member of the Pomatiopsinae. Connolly (1939) listed 10 species of *Tomichia* from South Africa but said nothing about their soft parts, morphology or ecology. On the basis of shell and radula data presented by Connolly (1939), I saw a resemblance between *Tomichia differens, T. natalensis,* and *T. cawstoni* and various species of *Tricula.* I thought that these species might, in fact, be species of *Tricula.* Accordingly, I initiated studies in South Africa in 1977 to 1) see if one or all of the three species in question were *Tricula,* thus strengthening the hypothesis of South Central Gondwanian origin of the Triculinae; 2) assess the extent of morphological divergence among species of *Tomichia* and *Tricula* that I might find there; 3) assess the extent of the *Tomichia* radiation; 4) learn about the ecology of the relevant species and, if possible, about the origin and radiation of *Tomichia.*

Methods of collection and dissection were those of Davis & Carney (1973) and Davis (1979). Collections were made from the Orange River, Namaqualand in the west beneath the escarpment along the entire coast of South Africa eastward to Richard's Bay near Mozambique (Appendix 1). All localities where snails were found are shown in Figs. 7, 8. Anatomical data and systematic analyses are given in Appendix 2. Types examined are discussed in Appendix 3. As a result of these data I have reduced the number of species of *Tomichia* in South Africa to seven (Table 3). The shells and distribution of these species

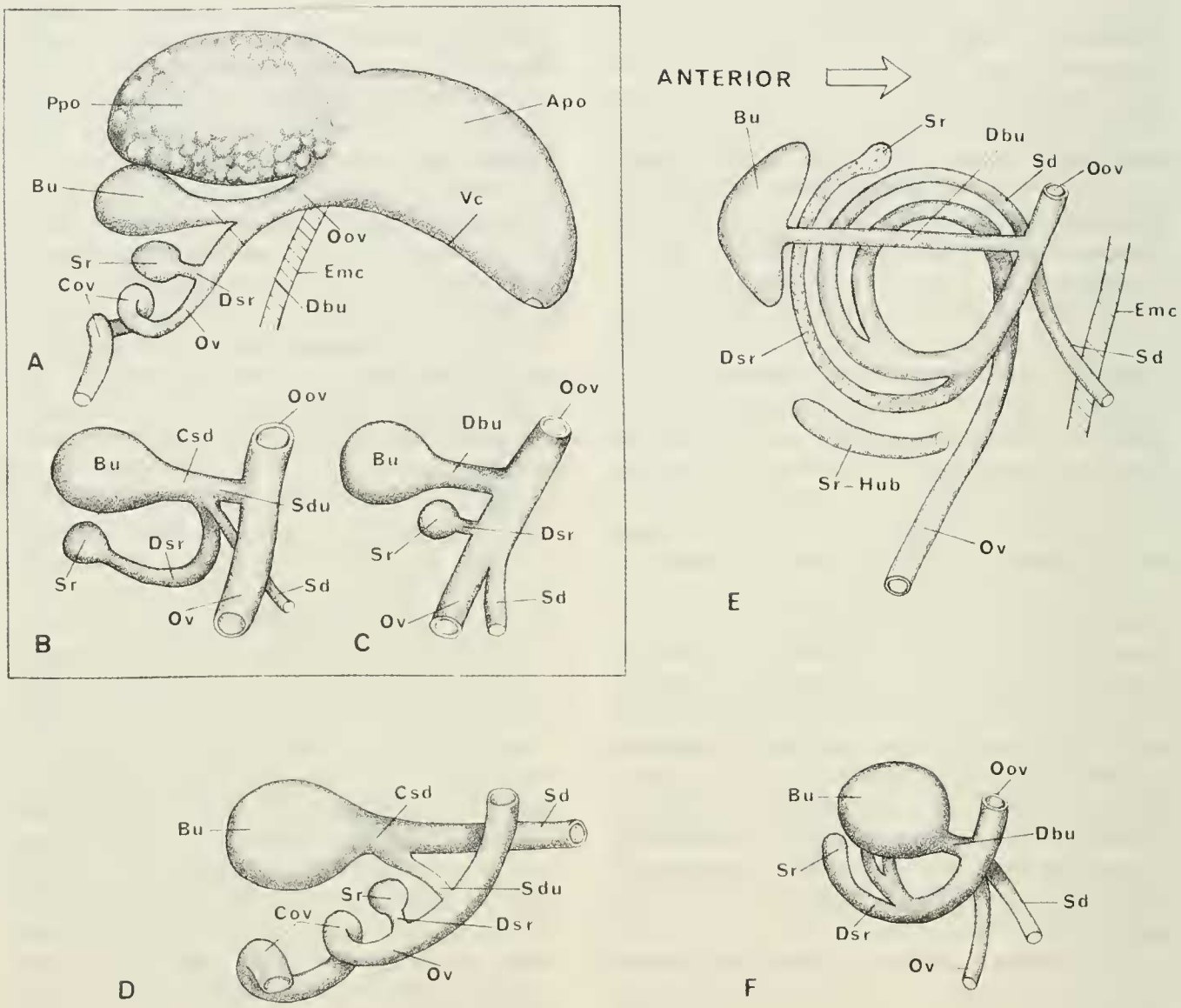

FIG. 6. Female reproductive system. The generalized character states are seen in the box: A, Hydrobiidae; B. *Tricula burchi, Tricula aperta*; C, *Tricula bollingi*. D, Pomatiopsinae. E, Derived oviduct circle complex of the Jullieniini. The short seminal receptacle of *Hubendickia* (Sr-Hub) is considered generalized; the elongate one (Sr), derived. F, *Karelainia*; a very condensed oviduct circle complex with short Sr.

Abbreviations: Apo, anterior pallial oviduct; Bu, bursa copulatrix; Cov, Coiled section of oviduct; Csd, common sperm duct; Dbu, duct of the bursa; Dsr, duct of the seminal receptacle; Emc, posterior end of the mantle cavity; Oov, opening of oviduct to Ppo; Ov, oviduct; Ppo, posterior pallial oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle; Sr-Hub, seminal receptacle of *Hubendickia*; Vc, ciliated ventral channel (from Davis, 1980).

are shown in Figs. 7 and 8. *T. cawstoni* is possibly extinct (see Appendix 3). *T. alabastrina* (Morelet) listed by Connolly (1939) is not a species of *Tomichia* but of *Hydrobia* s.s. (Davis, in prep.).

Morphological species concepts

Few morphological differences serve to separate the species (Appendix 2, Tables 4–6). *T. natalensis* and *T. differens* are unquestionably species of *Tomichia*. Those differences that do occur among species are primarily quantitative. The only morphological differences seen among species involve shell shape, size, tendency for shell microsculpture, position of the tip of the radular sac, very slight differences of point of entry of the spermathecal duct into the bursa copulatrix and slightly different positional relationship between the openings of the sperm duct and spermathecal duct into the bursa copulatrix.

FIG. 7. Shells and distribution of *Tomichia rogersi* (R), *T. ventricosa* (V), *T. tristis* (T), and *T. natalensis* (N). Further distributions of *T. ventricosa* are given in Fig. 8 with emphasis on the Agulhas area. The coastal stretch from East London to Durban is devoid of *Tomichia* because cliffs fall abruptly to the sea and deep eroded stream channels provide no suitable habitat. Also, this stretch has little or no calcium deposits (see Fig. 11). Shell sizes are given in Table 12. Numbers, e.g. V_1 refer to collection sites listed in Appendix 1. All shells are printed at the same scale.

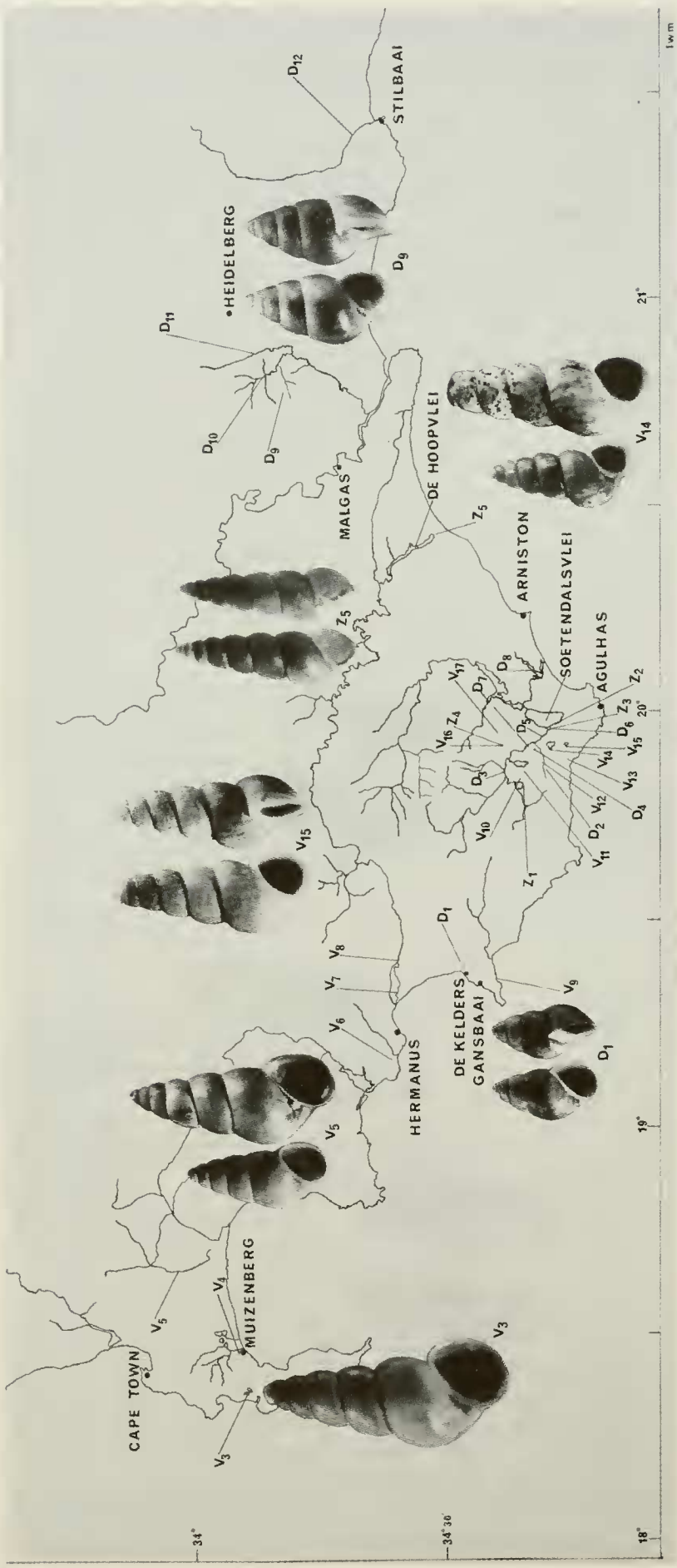

FIG. 8. Shells and distribution of *Tomichia ventricosa* (V), *T. differens* (D), and *T. zwellendamensis* (Z). Shell sizes are given in Table 12. Numbers, e.g. D_1 refer to collection sites listed in Appendix 1. All shells are printed at the same scale.

TABLE 3. South African species of *Tomichia* Benson, 1851.

Type-species: *Truncatella ventricosa* Reeve, 1842: 94, pl. 182, fig. 2, by monotypy.
Type-locality: South Africa, marshes of the Cape Flats.
Distribution of type-species: South Africa, coastal regions below the escarpment from Ysterfontein to Agulhas, Cape Province.
Species of *Tomichia* (+ = synonyms)

1. *T. cawstoni* Connolly, 1939. Kokstad, Cape Province
2. *T. differens* Connolly, 1939. Die Kelders, on coast of Walker Bay, about 10 mi. S of Stanford, Cape Province
3. *T. natalensis* Connolly, 1939. Lower Umkomaas, Natal Province
4. *T. rogersi* (Connolly, 1929). Stinkfontein, Namaqualand
   Hydrobia rogersi Connolly, 1929
5. *T. tristis* (Morelet, 1889). Port Elizabeth, Cape Province
   Hydrobia tristis Morelet, 1889
   + *T. lirata* (Turton, 1932). Port Alfred, Cape Province
   Assiminea lirata Turton, 1932
6. *T. ventricosa* (Reeve, 1942)
   +*T. producta* Connolly, 1929. Eerster River, Cape Flats, Cape Province
7. *T. zwellendamensis* (Küster, 1852). Lakes and streams in Zoetendol Valley, Bredarsdorp District, Cape Province
   Paludina zwellendamensis Küster, 1952: 53, pl. 10, figs. 19–20.

TABLE 4. Comparison of *Tomichia* species using 25 characters and their states. There is at least one difference among the species involving each character. Characters 18 to 24 involve scaling (see Table 6). In a two state character 0 = no; 1 = yes. NC, no data.

Characters and character states	*T.d.*	*T.n.*	*T.r.*	*T.t.*	*T.v.*	*T.z.*
1. Shell length based on length of last three whorls (see Fig. 12). a. small (0) b. medium (1) c. large (2)	0	0	2	1	1	0
2. Shell aperture shape a. ovate (0) b. ovate-pyriform (1) c. subquadrate (2)	1	2	0	0	0	0
3. Shell shape a. ovate (bullet-shaped) (0) b. ovate-conic (1) c. turreted (2)	0	1	2	2	2	2
4. Shell peristome brown-rimmed (0, 1)	0	1	0	0	0	0
5. Shell peristome complete and well-developed (0, 1)	1	1	1	1	1	0
6. Shell columellar twist evident (0, 1)	0	0	0	0	0	1
7. Shell outer lip thin (0, 1)	0	0	0	0	1	1
8. Shell spiral microsculpture a. none (0) b. on some shells (1) c. commonly seen (2) d. strong and producing malleations (3)	2	0	1	3	1, 2	0
9. Shell inner lip reflected a. not so (0) b. slightly (1) c. pronounced (2)	0	0	0	1	2	1

TABLE 4 (Continued)

Characters and character states	*T.d.*	*T.n.*	*T.r.*	*T.t.*	*T.v.*	*T.z.*
10. Radula central tooth formula $\frac{3-1-3}{2-2}$ (0) $\frac{2-1-2}{2(3)-(3)\,2}$ (1)	1	1	0	1	1	0
11. Radula cusps on outer marginal may be > 11 (0, 1)	0	0	0	0	0	1
12. Radula cusps on inner marginal may be > 13 (0, 1)	0	0	0	0	1	1
13. Tip of radular sac ventral to buccal mass (0, 1)	0	1	1	1	1	1
14. Sexual dimorphism in shell length (0, 1)	0	1	0	NC	NC	0
15. Shells of males and females a. have same no. whorls (0) b. males have more (1) c. females have more (2)	0	1	2	NC	NC	0
16. Spermathecal duct opens into the bursa: a. posterior end, <.35 mm from end (0) b. >.40, <.60 mm (1) c. >.70 (2)	1	0	2	1	1	1
17. Spermathecal duct opens into left ventrolateral edge of bursa (0, 1)	0	1	0	0	0	0
18. Pleuro-subesophageal connective longer than expected for body size (0, 1)	0	1	0	0	0	0
19. Body length relative to shell length a. longer than expected (0) b. shorter than expected (1) c. as expected (2)	2	2	2	0	1	2
20. Length radula/length of buccal mass a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	0	2	1	2	2
21. Length of bursa/length of pallial oviduct a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	0	2	2	2	2
22. female gonad a. longer than expected (0) b. shorter than expected (1) c. as expected (2)	1	2	2	2	2	2
23. Length of pleurosupraesophageal connective a. greater than expected (0) b. less than expected (1) c. as expected (2)	2	2	2	2	2	1
24. Gill filaments (male and female) a. more than expected (0) b. fewer than expected (1) c. as expected (2)	2	2	2	2	2	0
25. Gill filament no. sexual dimorphism (0,1)	0	1	0	0	1	0

There are differences in the number of gill filaments. A number of quantitative differences are seen once data are arranged to permit scaling (Table 6). We do not see the kind of shell shape and sculptural diversity that is common among species of various triculine genera. We do not see any cladogenesis.

Discussion of relationships

On the basis of the morphological data (Tables, Appendix 2), 25 characters and their character states serve to discriminate among species (Table 4). As seen in Table 5, species differ by as few as seven (28%) and as many as 20 character states (80%). Of these characters, 9 (36%) involve shell characters, 4 (16%) involve radular characters, 3(12%) relate to sexual dimorphism (shell, gill filament number), 2 (8%) are internal anatomical features involving the bursa copulatrix and 7 (28%) involve scaling (Table 6)—comparisons of all species to assess whether or not the number and/or size of organs/structures correlate with overall size.

TABLE 5. Number of differences among species of *Tomichia* based on data in Table 4.

	T.d.	*T.n*	*T.r.*	*T.t.*	*T.v.*	*T.z.*
T. differens	—	14	9	9	10.5	14
T. natalensis		—	14	13	14	20
T. rogersi			—	7	8.5	12
T. tristis				—	7	12
T. ventricosa					—	11
T. zwellendamensis						—

Aside from shell size and shape, the species do not differ much from each other. There are only two qualitative differences of internal morphology, i.e. clearly seen changes in structure or position of organs or structures. These are the position on the bursa where the spermathecal duct joins the bursa; the position on the bursa where the sperm duct joins the bursa. All other differences are quantitative and the seven character-state differences involving scaling necessitated a careful comparison of all species for all measurements to uncover subtle differences.

In analyzing data for scaling (Table 6) trends are looked for that clearly deviate from the expected. Expected trends are: 1) a de-

TABLE 6. Species ranked in decreasing shell size based on length of the last three whorls in order to assess if size or numbers of structures correspond to overall size based on shell size.

Species	Length of last three whorls	Length of body (♀)	Length of buccal mass	Length of radula ÷ length of buccal mass	Length of bursa copulatrix ÷ length of pallial oviduct	Length of bursa copulatrix
T. rogersi	6.8 ± 0.18	12.3 ± 1.1	1.3 ± 0.1	1.07	.36 ± 0.04	1.70 ± 0.11
T. tristis	5.7 ± 0.29	12.6 ± 1.8*	1.3 ± 0.1	0.95*	.32 ± 0.02	1.41
T. ventricosa	5.3 ± 0.48	8.7 ± 0.6*	1.0 ± 0.2	1.06	.31 ± 0.07	1.18 ± 0.15
T. differens	4.3 ± 0.14	8.3 ± 0.4	1.0 ± 0.2	1.26* 1.19	.31 ± 0.04*	1.11 ± 0.11
T. zwellendamensis	4.1 ± 0.19	8.4 ± 0.8	0.9 ± 0.2	1.08	.29 ± 0.04	1.09 ± 0.23
T. natalensis	4.1 ± 0.22	8.2 ± 0.6	0.9 ± 0.02	0.98	.40 ± 0.02*	1.26 ± 0.06*

	Length of ♀ gonad	RPG ratio	Length of pleuro-supraesophageal connective	No. of gill filaments ♂	No. of gill filaments ♀	Length of pleuro-subesophageal connective
T. rogersi	2.26 ± 0.3	.61 ± .06	.62 ± .15	51 ± 4	52 ± 3	.08 ± .11
T. tristis	2.0 ± 0.2	.61 ± .09	.50 ± .09	58	56 ± 3	.13 ± .15
T. ventricosa	1.23 ± 0.3	.54 ± .04	.42 ± .09	40 ± 3	55 ± 2**	.04 ± .05
T. differens	1.05 ± 0.3*	.49 ± .06	.30 ± .07	28 ± 3	29 ± 3	.03 ± .03
T. zwellendamensis	1.3 ± 0.1	.51 ± .07	.23 ± .07*	66*	51 ± 8	.02 ± .02
T. natalensis	1.20 ± 0.2	.57 ± .04	.36 ± .03	30	38 ± 2**	.14 ± .07*

*Pronounced departure from the expected trend.
**Sexual dimorphism noted.

crease in body length as shell length decreased, 2) a correlation of decrease in organ length with body length decrease, 3) an optimal size of organ length over a range of body lengths, 4) the decrease of organ length with body length until a constraint is reached where the organ could not function properly at a smaller size. With regard to the expected trends we see in Table 6 that buccal mass length fits the class 3 expectation above and there is no significant difference among the four smallest species. On the other hand one notes, examining columns 3 and 4, that the fourth smallest species has a ratio of length of radula divided by length of buccal mass that is significantly greater than that seen in any other species, larger or smaller; also, the smallest species has a much larger ratio of length of bursa copulatrix divided by length of pallial oviduct (column 5) than all but the largest species. Other departures from the expected are marked in Table 6.

There are no pronounced radular differences (Figs. 9, 10). There is variability in central tooth center cusp width but very little in cusp number. There are none of the profound

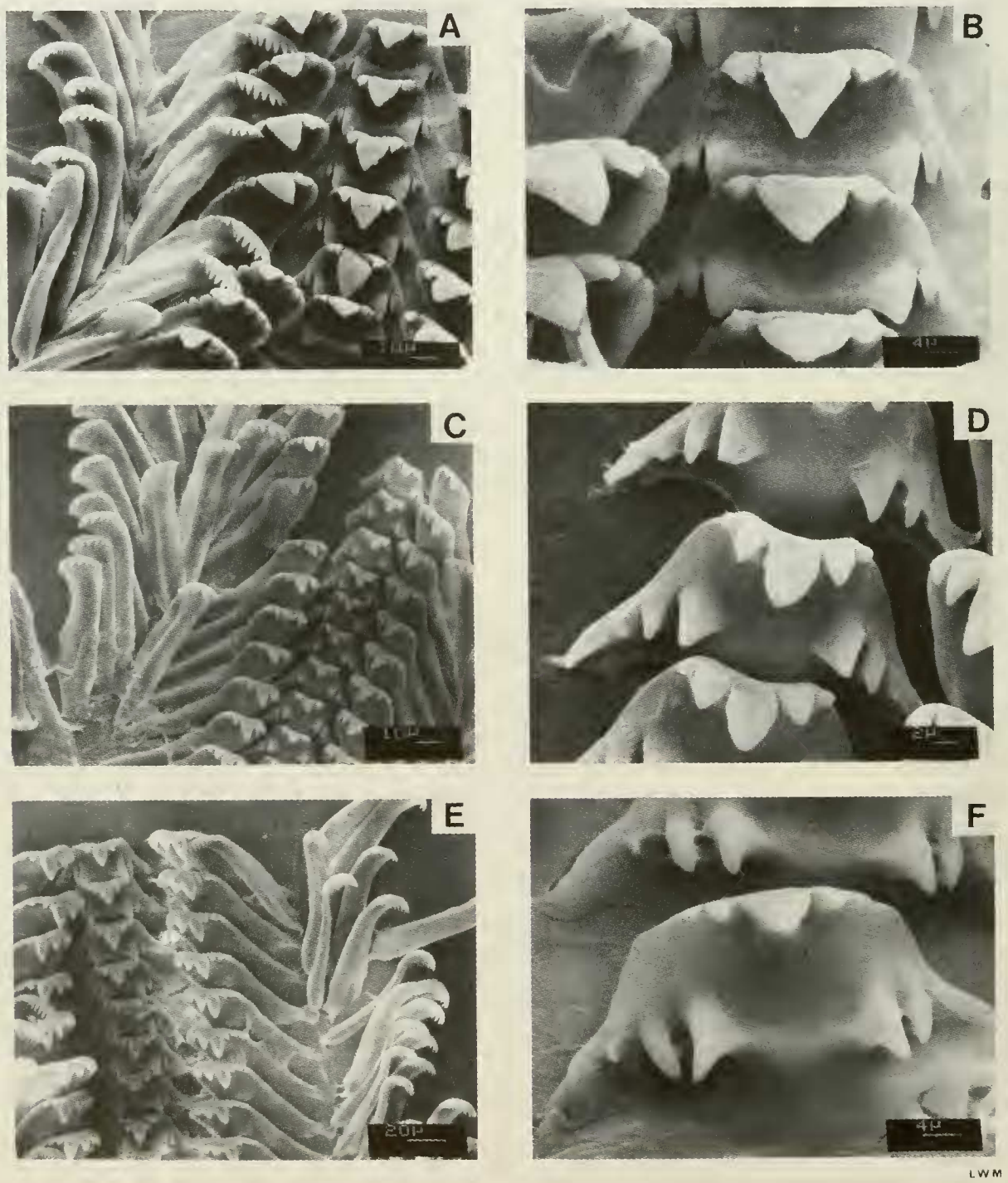

FIG. 9. Scanning electron micrographs of radulae A, B. *Tomichia differens* (D77-13); C, D. *T. natalensis* (D78-212); E, F. *T. rogersi* (D77-20).

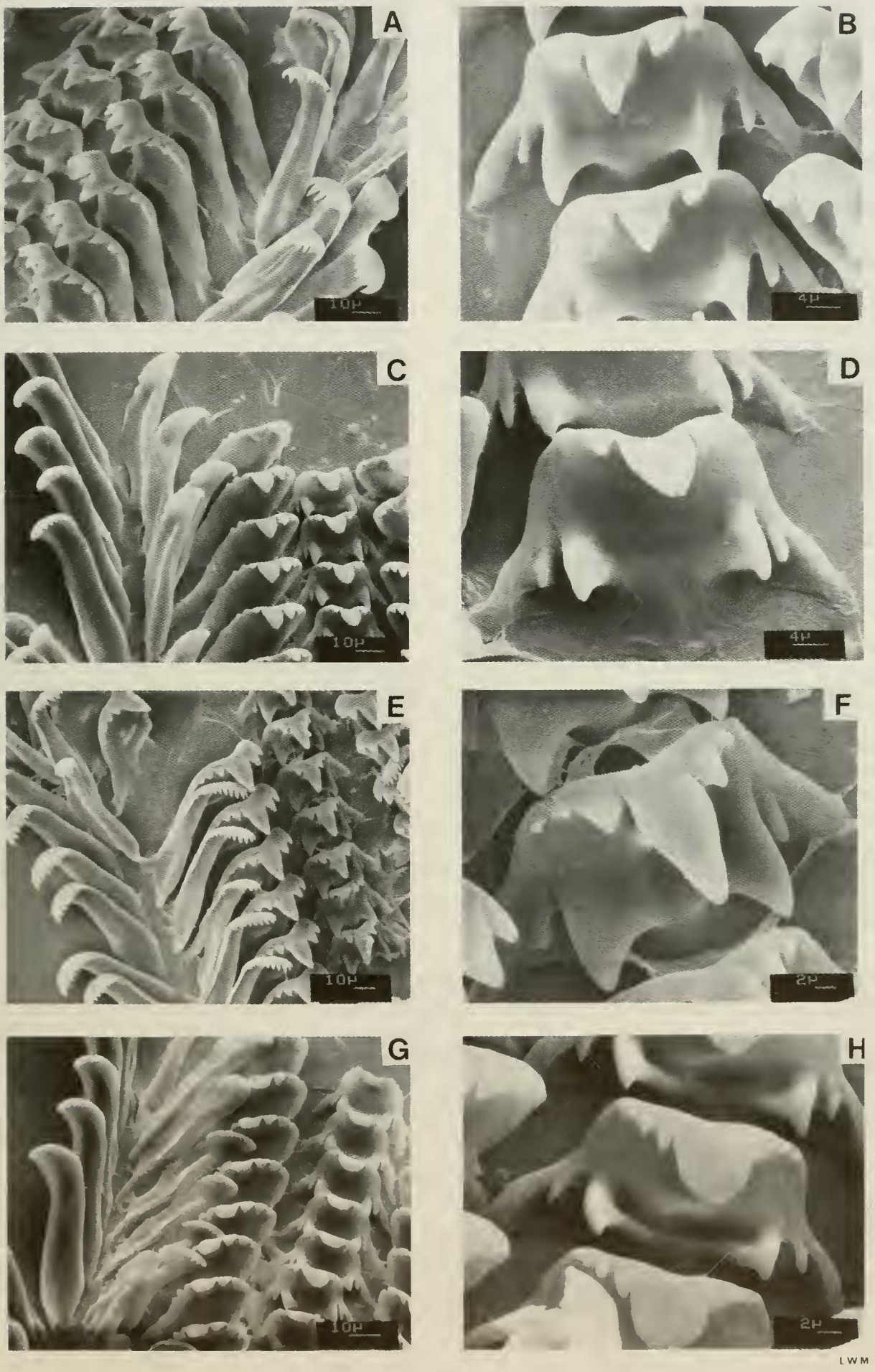

FIG. 10. Scanning electron micrographs of radulae. A, B. *Tomichia tristis* (D78-53); C, D. *T. ventricosa* (D77-16); E, F. (D78-80); G, H. *T. zwellendamensis* (D78-74).

differences in structure marking different modes of feeding as seen in the *Hubendickia* or *Hydrorissoia* radiations (Pomatiopsidae: Triculinae) in the Mekong River (Davis, 1979: fig. 4). The variation in cusp number is not impressive considering the notorious variability recorded for pomatiopsine populations or subspecies of *Oncomelania hupensis* and *Pomatiopsis lapidaria* (Davis & Carney, 1973; Davis, 1967).

The anterior central cusp of the central tooth may be narrow and elongate in some individuals of some populations of *T. ventricosa* (Figs. 10E, F). Only one in nine individuals of the V_1 populations had this morphology while 90% of the individuals from V_{15} had the narrow cusp. Refer to Connolly (1939: fig. 48) for figures of radulae of taxa considered species by him. He considered that there were distinct radular types. I conclude from this study that variation within one or two populations of *T. ventricosa* encompasses most of the types considered distinct by Connolly.

One of Connolly's taxa requires special comment. *T. producta* Connolly was named with the Eerste River, Cape Flats, Cape Province, as type locality. The species differed from *T. ventricosa* by more rounded whorls, deeper sutures, and tall turreted spires of up to 10 whorls. The anterior central cusp of the central tooth was very broad contrasting the narrower cusp seen in *T. ventricosa*. Variability in cusp diameter has been discussed. Shells matching Connolly's figure (1939: fig. 47D) are seen most frequently in pans as defined earlier in this paper. The form is especially seen in the pans near Zoetendalsvlei. No data support consideration of this form as a distinct species; it represents part of the variability of *T. ventricosa*.

Considering the minor differences that do occur among species it is clear (Table 5) that *T. ventricosa, T. tristis,* and *T. rogersi* have the greatest similarity, with *T. differens* clustering close to these three species. *T. natalensis* and *T. zwellendamensis* are distinctly divergent from each other and from the cluster containing the other four species. *T. zwellendamensis* shares more character states in common with *T. ventricosa; T. natalensis* is closest to *T. tristis*.

Ecology

The greatest differences seen among species of *Tomichia* are physiological differences not morphological ones. These differences, summarized in Table 7, are discussed below.

Tomichia ventricosa—This species lives in the broadest range of environments seen for any species of *Tomichia*. The species is found in shallow rivers (H_2O, 0‰), coastal wetlands and estuarine settings with low salinity (4–8‰). *T. ventricosa* is also found in vleis and pans where the basin fills with water during the rainy season and dries out slowly during the dry season, often becoming totally dry for varying periods of time, i.e. weeks to months. With the onset of rain, water in the newly filled basins has a salinity (8–10‰); as they dry out the water becomes increasingly saline (to >160‰).

The river populations apparently live con-

TABLE 7. Habitat types and salinity measurements from habitats where species of *Tomichia* were found.

Species of *Tomichia*	Habitat	Salinity (American Optical Refractometer)
T. cawstoni	species extinct?	—
T. differens	aquatic	$\bar{X}$, 2.3‰ (0–4‰; 1 locality, 9.5‰), N = 11
T. natalensis	amphibious, stream banks	stream 0‰, N = 4
T. rogersi	aquatic, amphibious	(4–5‰), N = 2
T. tristis	terrestrial, amphibious; high above shoreline of aborted estuary	lagoon 20‰, N = 1
T. ventricosa	aquatic, amphibious, rivers	(4–8‰), N = 2
	vleis	$\bar{X}$, 34‰, (8–83‰), N = 9
	pans	(25–32‰), N = 2
T. zwellendamensis	aquatic in vleis, lakes	$\bar{X}$, 2.6‰ (0–8‰), N = 5

tinuously submerged in perennially flowing water. It is probable that the rivers of Sandvlei, Muizenberg (D77-50) and Kleinrivier near Hermanus (D7) occasionally do dry up during periods of severe drought but I saw no evidence for this. I have collected living specimens of this species in only two rivers.

The situation in temporary standing water vleis and pans is in stark contrast to that in perennial rivers. Pans are circular and rain-filled shallow pools most frequently seen near the shore behind the foredunes of the Cape Province, especially near Agulhas and Hermanus. Vleis are irregularly shaped catchment basins or playa lakes often associated with streams and small rivers that go dry annually or, in some cases, irregularly. Because of their proximity to the sea and the evaporative cycle, pans and vleis are saline as evidenced by the *Salicornia*-rich fringing vegetation. The cycle involving *Tomichia ventricosa* is shown by a study of this species at Ysterfontein Vlei in the Cape Province (refer to Tables 8, 9). I first visited the vlei on 15 November 1977 and it was nearly full of water with 12‰ salinity. Snails were found under rocks near the edge of the water. Blooms of coarse-stranded green algae were starting. I marked the high water point and returned on 30 December 1977 during which time the water had receded horizontally 26 m and the salinity had more than doubled. Snails were found in hundreds per m^2 in the shallows, on the substrate and in algal masses that had accumulated. The snails did not appear in the least affected by the salinity approximately equal to that of the offshore ocean water. I also took soil-substrate samples (400 cm^2) at intervals between the water and the high-water mark and found that over 92% of the snails found in the samples were living (Table 9).

On the 4th of February, 1978, the water had receded another 15 m and the salinity was approximately double that of sea water. Snails were found concentrated as before. Out in the Vlei, salt crystals were encrusting the algal mats exposed to the sun (83‰) but the snails were moving about normally. On shore where the water had retreated, algal

TABLE 8. Record of the drying up of Ysterfontein Vlei (V_1, D77-11) and the associated increase in salinity.

Date	Meters from first highwater marker to edge of water	Salinity (‰)
15 November 1977	0	12
30 December 1977	26	28
4 February 1978	41 (edge H_2O)	58
	91 (out in shallow H_2O)	83
March 1978	>.8 km	>160
April 1978	>.8 km	>160

TABLE 9. Snails, living and dead, sorted from small substrate samples (soil to 2″, grass, *Salicornia* spp., rocks) taken from three localities along a transect from the 15 November 1977 high water mark to the edge of the water, 26 m away at Ysterfontein Vlei; see Table 8; 30 December 1977.

	7.3 m (from high water mark)		16.5 m		21 m	
Size class (mm)*	Living	Dead	L.	D.	L.	D.
<1.84	4	0	20	0	26	0
1.84–1.96	14	1	16	0	15	1
2.00–2.20	25	1	13	1	33	0
2.24–2.44	30	1	18	2	25	0
2.48–2.68	15	0	16	0	21	0
2.72–2.92	12	2	12	0	12	1
2.96–3.16**	1	0	3	0	2	0
>3.20	1	3	2	0	2	0
	102	8	100	3	124	2
% living	92.7		97.1		98.4	

*length of body whorl

**size class for $\bar{X}$ of mature males and females used for anatomical studies: Appendix 2, Table 12.

masses had settled on the *Salicornia* and *Arthrocnemum* plants forming a continuous thick, tough, dry roof separated from the substrate by 3 to 8 cm. Upon cutting open a hole in the algal-mat roof one could see active snails on the moist substrate below. The snails were amphibious in this humid, moist environment.

I also watched the drying up of the Vermont Pan near Hermanus. As long as there was water in the pan, snails were seen crawling about on the compressed sandy substrate; there were hundreds per m^2. There was little fringing *Salicornia* and/or *Arthrocnemum* and no masses of algae in the water. When the pan was dry and sunbaked, the edge of the pan was ringed with windrows of dead *Tomichia ventricosa* shells. Upon pulling up rocks and digging down along fissure-like cracks I collected snails that, upon being placed in water, were found to be living. It was thus evident that snails could survive by burrowing below the surface to areas harboring some moisture, and survive there in estivation until the next rain.

In yet another pan near Agulhas, the substrate was packed sand and the water level was nowhere greater than 15 to 20 cm deep. The salinity was 25‰ and snails were of approximately the same density on the substrate as in the Vermont Pan. The banks of the pan were packed sand and at the high water mark were windrows of dead snails with some piles 20 to 30 cm deep with thousands of *T. ventricosa* shells.

No other snails are capable of living in the vleis and pans inhabited by *T. ventricosa*. *T. ventricosa* that survive the period of desiccation emerge during the rainy period into an environment filling with freshwater where salinity levels probably reach 9 to 10‰. It is most likely that at this time they reproduce with exceptionally high intrinsic rate of natural increase (r). With the dry season the snails adjust to dwindling water and increasing salinity until they are forced into an amphibious mode of existence or into estivation. Snails not reaching safety within the moist chambers provided by *Salicornia* plants and algal-mat roofs or beneath rock piles or other subterranean refuges die due to stranding and desiccation or by osmotic death when the remaining pools of water reach a salinity of 130 to 160‰ (as in Ysterfontein Vlei, March and April, 1978; see Table 8).

Tomichia ventricosa has adapted to the greatest range of environmental conditions and stresses of any species of snail I know: freshwater, brackish to hyper-saline, amphibious, dry substrate estivation.

T. differens—This species is found living in streams and small rivers with perennial water. At the type-locality this species lives on rocks, feeding on algae and algal-associated material under a thin sheet of continuously flowing water (5 mm to 3 cm depth). The stream is an outflow from a limestone cave, some 5 to 6 m above sea level; the distance from the cave opening to the sea is some 20 to 25 m. The species is common along the base of aquatic sedges in the Nuwejaarsrivier (River) flowing into Soetendalsvlei, a large lake near Agulhas. In other areas (Appendix 1, D11) this species is common in and on algal mats in a small stream. At one locality (Appendix 1, D4) near Soentendalsvlei, the species was common in a small stream on 1 January 1978, the stream had dried up but the snails were alive under stones and rocks. This stream flows into the Nuwejaarsrivier and on 19 January 1978, this species was still common in this river and water levels in the river were only slightly lowered from levels seen on 1 January 1978.

The salinity of the water was 0 to 4‰ in 10 of 11 habitats tested; 9.5‰ in only one habitat (Table 7; Appendix 1). I consider *T. differens* to be a freshwater aquatic species living in perennially flowing waters. It probably has some capability for withstanding desiccation for a limited period of time.

T. natalensis—This species is only found in Natal; it is primarily amphibious on stream banks with mud slopes of 45° or less and in considerably shady and humid environments provided by grassy vegetation. The habitat is a cross between that seen for *Pomatiopsis lapidaria* and *P. cincinnatiensis* of the eastern United States (Van der Schalie & Dundee, 1955, 1956; Van der Schalie & Getz, 1962, 1963). In one location (Appendix 1, N3) snails were exceedingly numerous among and under stacks of soggy reeds; many of the snails were obviously living submerged while others were out of water. The water always had 0‰ salinity.

This species was only found in the Zululand region of Natal. Widespread sugar cane farming in upland and coastal Natal has had a profound negative impact on streams there. The few remaining habitats of *T. natalensis* are, in fact, bounded by cane fields and their future is insecure.

T. rogersi—This, the largest species of

Tomichia, is found in only two localities, isolated from each other in the high desert of Namaqualand. The species is freshwater-aquatic with some tendency towards being amphibious. In Lekkersing, a tiny community of human desert dwellers, this species is located in a blind canyon with only a single small spring for water. The spring was capped with a stone base and windmill. From the base of the windmill, a tiny trickle of water has resulted in a seepage channel some 23 m long that ends in sand. The seepage supports a narrow grassy strip about 0.6 m on each side. The soil is only damp as there is insufficient water to maintain any visible surface flow. Snails are numerous among and under rocks and among the basal grass stems along the seepage channel.

The habitat at Eksteenfontein, the second locality, is rather similar except that the spring is larger and the flow of water produces a visible stream. Where the water flows through coarse grass, snails are abundant at the stems of the grass at the mud-emergent grass interface just at water level, not submerged in water.

A search of remaining isolated springs in Namaqualand, e.g. Khubus (28° 28′ S.; 17° 00′ E.) or Annisfontein (28° 25′ S.; 16° 53′ E.) either yielded no snails or only the pulmonate *Bulinus.*

T. tristis—I consider this species to be terrestrial-amphibious. I found the species in only one locality (Appendix 1, T), along the west bank of the large lagoon at Aston Beach, Cape Province. The bank was near the junction of Seekoeirivier (River) and the lagoon, and close to human habitation. The snails were not in a marshy area, but high up on the shore, in a well drained area next to the mowed lawn of the residence. The snails were on black loam beneath branches, logs and piles of similar debris along with a species of *Assiminea.* The habitat was moist and humid but not wet. It was evident on the basis of a healthy terrestrial environment that this locality was only rarely flooded. The snails were numerous, reaching hundreds per m^2 but patchy, being found only under trash, brush or logs. Water of the lagoon some meters away was 20‰. There were no snails of any kind among the *Salicornia* plants at waters edge or in the lagoon.

T. zwellendamensis—This species is freshwater-aquatic living on stems of sedges or on the bottom of lakes and ponds, not in fast flowing water, of the Agulhas area. The species is particularly abundant near the opening into Soetendalsvlei and in De Hoopvlei, a large lake along the road from Aguihas to Potbergsrivier (Appendix 1, Z5). In the Hoopvlei, snails were hundreds per m^2 on the marl-sandy bottom and algal patches. They live in permanent lakes or ponds of water with 0 to 8‰ salinity (Table 7).

Sympatric Species

I have found sympatry in only two localties involving three species: *T. differens, T. zwellendamensis,* and *T. ventricosa. T. differens* and *T. zwellendamensis* were found in a pan next to the Nuwejaarsrivier just before the river emptied into Soetendalsvlei (Appendix I, D6, Z3). The depth of water in the pan was 5 cm, the bottom was of marl and the water rather muddy (not due to any recent rain). The edge of the pan was some 3 m from the river. *T. zwellendamensis* was common in grass on the bottom. There was an occasional *T. differens* among them. *T. differens* was common in the river on the stems of rushes and sedges while there were very few *T. zwellendamensis* in that habitat.

The other locality showing sympatry was a few miles from Soetendalsvlei, i.e. Longepan (Appendix 1, V17; Z4). *T. ventricosa* was common in the main part of the vlei, both on sedges and the sandy bottom. *T. zwellendamensis* was located where the vlei exited, flowing to the east, on the stems of reeds in quiet water. The salinity of the water in the vlei was 8‰.

DISCUSSION

In this section I discuss 1) the proposition that no concrete evidence supports the origin of *Tricula* on the African plate, 2) the age and distribution of *Tomichia* in South Africa, 3) the effects of changing environment on *Tomichia,* 4) preadaptive features in Pomatiopsinae for an amphibious or terrestrial existence, and 5) the tempos and mode of pomatiopsine evolution.

African *Tomichia* and the *Tricula* question

There are three species considered to be *Tomichia* that occur in central Africa (Brown, 1980). Verdcourt (1951) placed his *Hydrobia hendrickxi* from Kakonde, E. Zaire, in the genus *Tomichia* because of the morphology of the central tooth of the radula. *Tomichia*

was characterized by a peculiar raised basal projection of the central tooth giving the impression of a transverse line across the face of the tooth (Connolly, 1939; Verdcourt, 1951). The natural affinities of these central African taxa, removed some 2000 miles from the South African radiation, cannot be clarified without a thorough anatomical study. In attempts to learn more about the evolution of *Tomichia* it will be essential to study these taxa in detail to learn if they are, in fact, *Tomichia,* and to determine the degree of morphological relationships to South African *Tomichia.*

The transverse bar across the face of the central tooth is clearly illustrated in Connolly (1939) and by Davis (1968) in describing new species of *Tricula* from northwestern Thailand. On the basis of this basal bar and shell morphology it seemed certain that at least *Tomichia cawstoni, T. natalensis,* or *T. differens* would be, in fact, members of the tribe Triculini (Davis, 1979). On the basis of the anatomical data this is clearly not the case. The shells and radulae of certain *Tricula* and the above named species of *Tomichia* are extremely similar yet they belong in different subfamilies given their overall morphology. Accordingly, the relationship of *Hydrobia hendrickxi* to various pomatiopsid taxa is quite uncertain. Shell and radula alone are not sufficient for assessing relationships.

The so-called basal bar on the central tooth is a weak and uncertain character. The SEM pictures of the central tooth (Figs. 9, 10) do not reveal such a structure. Reexamining these radulae with transmitted light microscopy reveals the line but at a focal plane beneath the surface of the face of the tooth. Thus there is no pronounced ridge on the face of the tooth; the line is a subsurface structure. What is characteristic of the *Tomichia* central tooth is the extreme development of the inner pair of basal cusps that swell out far above the face of the tooth (well illustrated in Fig. 10B). So great is the outgrowth of these basal cusps that they often appear connected by a ridge (Fig. 10H), but this ridge is not in the same place as the illustrated basal line (Connolly, 1939). Another prominent feature of the *Tomichia* central tooth is the deep cavity beneath the basal cusps bounded by the lateral angle (see Fig. 10D or H).

There is no evidence substantiating the hypothesis (Davis, 1979) that there are Triculini in Africa. The amazing similarity in shell and radula discussed above among certain species of *Tomichia* and *Tricula* may reflect a common ancestry in the Cretaceous but no morphologically defined Triculini have been found in Africa to substantiate this contention. The similarity could just as well reflect ecology. This weakens the hypothesis that the Triculinae and Pomatiopsinae diverged from a common ancester but does not, in light of other morphological characters and their history as hosts of parasites compel one to reject a common ancestor.

Age, modern distribution, man and the *Tomichia* radiation

The present coastal configuration of southern Africa was established by the end of the Cretaceous (Tankard et al., 1981). The fossil record of the Upper Cretaceous of South Africa and northern India reveals the presence of freshwater hydrobioid snails that were, with high probability, precursors of modern Pomatiopsidae (Davis, 1979). At that time when we first can track early Pomatiopsidae, they are freshwater-aquatic. The earliest record we have of the modern *Tomichia* radiation is from the Pliocene, in particular from Varswater Formation of Langebaanweg (west of Ysterfontein Vlei, Cape Province) (Kensley, 1977). Of particular interest are the freshwater species among the 20 gastropod, 2 bivalve and 1 chiton species found. *Tomichia ventricosa* was found with the freshwater limpet *Burnupia capensis* (Walker), the discoidal planorbid *Ceratophallus natalensis* (Krauss), and the spired planorbid *Bulinus* cf. *tropicus* (Krauss). The shells of *T. ventricosa* were fragmented (possibly implying transport) while the fragile planorbids and limpet shells were beautifully preserved.

There was a marine transgression in the Pliocene. There is evidence for freshwater and estuarine environments behind dunes (Tankard, 1975; Tankard et al., 1981). The juxtaposition of marine, estuarine, and freshwater species indicates an environment similar to that seen today along the Cape Province coast, e.g., the Hermanus estuary. Evidently, a river flowed into a lagoon, which opened to the sea. Quiet freshwater pond-like areas adjacent to and connected with the river would provide a habitat suitable for the planorbids. There are also numerous remains of the aquatic plant *Chara* that suggest such a habitat. *Tomichia* would perhaps have lived as seen today in the river flowing into the Hermanus lagoon (Appendix 1, 7, D77–29).

These data strengthen the hypothesis that the modern *Tomichia* radiation began with freshwater snails in a perennial freshwater environment.

There are to my knowledge no fossils of other Miocene to post Miocene species of *Tomichia* of South Africa. The modern physiological radiation probably evolved starting in the Pliocene with the full establishment of aridity in western South Africa and the effects of aridity spreading eastward.

Two major factors besides aridity apparently affect the distribution of *Tomichia* in South Africa: calcium availability and man. The distribution of calcretes in South Africa are shown in Fig. 11 as adapted from Netterberg (1971). A calcrete is a material formed by calcium carbonate deposited from soil water. Areas that show absence of calcification are marked on the map. *Tomichia* is limited to the narrow coastal strip associated with the short drainage systems beneath the escarpments above which are desert or semi-desert conditions. *Tomichia* is not found in areas that are calcium deficient (compare Figs. 7, 8, and 11).

Of particular interest is the area between the Hoopvlei and Jeffrey's Bay (21° 30′ to 24° 30′ E. longitude). This strip of coast includes the Knysna-Wilderness lakes. Initially, I expected to find *Tomichia* here because there was an abundance of perennial freshwater involving lakes and streams connecting lakes. These lakes and rivers are, from west to east, Touwsrivier (= Touws River) emptying at Wilderness (salinity 4‰) Island Lake (= Eilandvlei) (7‰), Longvlei (10‰), Rondevlei (16‰); then draining to the east Swartsvlei (13‰), Groenvlei (3‰). The Karatararivier (River) flowing into Ruigtevlei that in turn flows into Swartsvlei had a salinity of 1‰. No *Tomichia* were found; a limpet was found in Groenvlei and numerous *Hydrobia* were found in Swartsvlei. No gastropods were found in any of the lakes or rivers except those mentioned.

The history of these lakes relates to fluctuations of land and sea level from the upper Pleistocene with a major marine transgression within the past 7,000 years. During periods of low sea level, the lakes were probably dry; the Recent lakes were probably formed by reflooding (Martin, 1962). In summary, calcium deficiency and the Recent history involving marine transgression in a series of basins originating in the upper Pleistocene are sufficient to explain the absence of *Tomichia*. *Tomichia* sp. recorded from the Pleistocene fossil deposits on terraces above the present lakes (Martin, 1962) are undoubtedly *Hydrobia*.

Man has had a profound influence on the

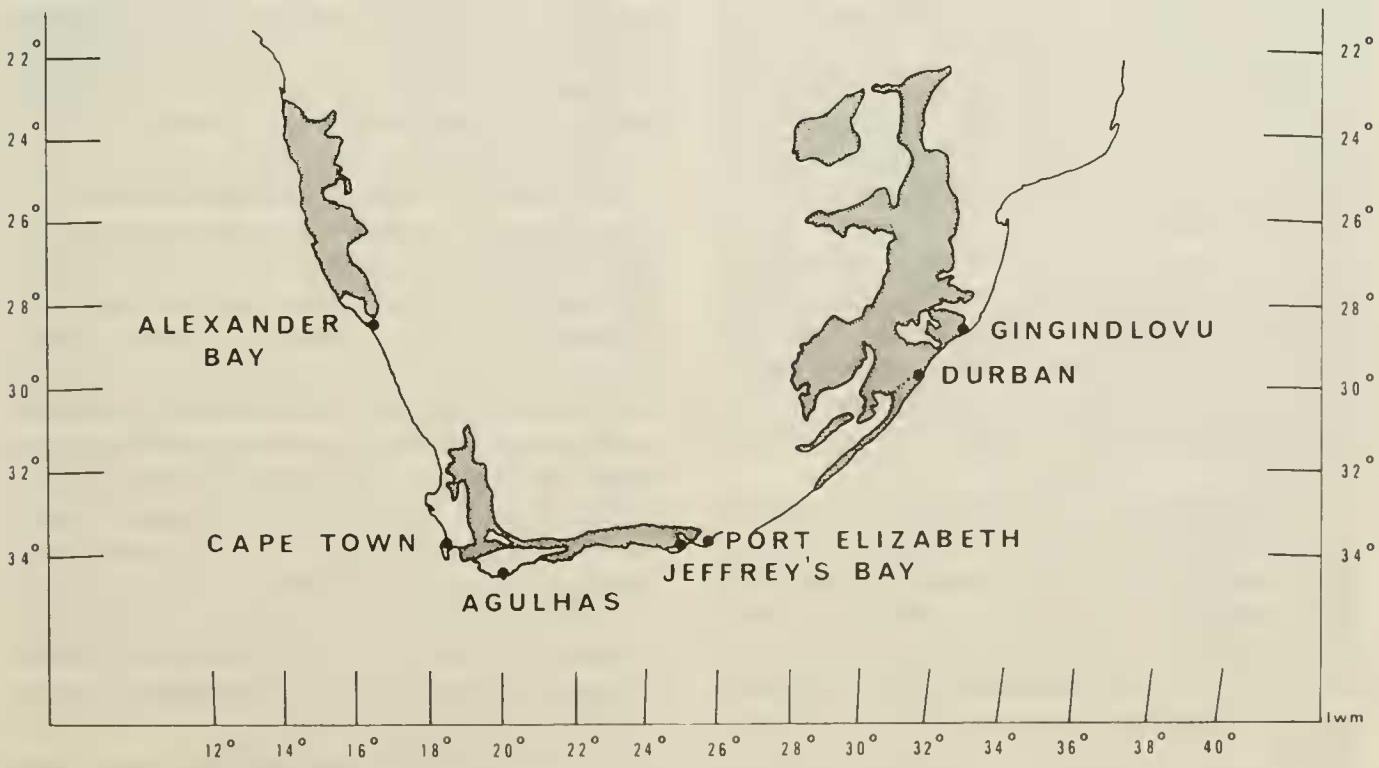

FIG. 11. Distribution of calcium deposits in South Africa. The shaded areas lack calcium deposits or calcretes (adapted from Netterberg, 1971).

distribution of *Tomichia*. Species of this genus are extremely sensitive to changes in their ecosystems relative to pollution of all types as well as interferences in the natural dry-wet seasonal cycles.

Only dead shells of *Tomichia* are now to be found in classic sites of Kuils River (34° 01′ S.; 18° 39′ E., near Cape Town Airport), Wild Bird Vlei, Cape Peninsula (34° 08′ S.; 18° 21′ E.), Kommetjie Vlei (34° 09′ S.; 18° 20′ E.), Reitvlei (33° 30′ S.; 18° 30′E.). We found extensive evidence for organic pollution in Kuils River. In Wild Bird Vlei, a sewage plant now makes use of the limited available freshwater. Where there once was a healthy ecosystem, one now finds a series of hypersaline ponds of about ⅓ normal volume (judged on the basis of the obvious basin that was filled a few years ago) with salinity >150‰, stinking black mud, numerous dead fish. Kommetjie Vlei has been drained off; Reitvlei was dredged out some years ago to supply fill to make the docks at Cape Town. Instead of a shallow vlei there is a large, deep artificial pit. Numerous subfossil shells are found on the northern shore above the high water line.

Environment and the modern *Tomichia* radiation

We see today in the Agulhas region of Cape Province, South Africa, what was common throughout South Africa in the Eocene into the Miocene, i.e. an abundance of perennial freshwater. I assume, on the available evidence, that proto-*Tomichia* of the Eocene was aquatic, abundant, and widespread. In the one area of South Africa where there is still an abundance of freshwater, i.e. the Agulhas area, there are numerous lakes, streams, and ponds and rivers of low salinity, but of suitable alkalinity for hydrobioid snail life. It is here that one finds the greatest concentration of snail-rich habitats and species, two of which are freshwater-aquatic in perennial systems with salinity ≤9‰; mostly 0–5‰.

It is evident that the *Tomichia* radiation is species poor compared with the Southeast Asian Triculinae radiations involving *Hubendickia, Pachydrobia,* etc. The *Tomichia* radiation is a physiological-ecological radiation, not one characterized by morphological changes. What accounts for this radiation?

The most plausible explanation is the progressive desertification in South Africa since the late Eocene, some 39 million years ago when temperate rain forests in Namaqualand became depleted and replaced by mixed sclerophyllic vegetation (Axelrod & Raven, 1978). There has been progressive climatic change. There has not been a history of tectonic change in the Cenozoic that is associated with morphological changes and explosive speciation events seen elsewhere.

The Mesozoic break-up of Gondwanaland caused changing patterns of ocean currents and climatic processes causing progressive aridity in South Africa. These changes are related to the history of glaciation at high latitudes, especially Antarctic glaciation (Tankard et al., 1981). While glaciation in Antarctica persisted throughout the Oligocene, its present thickness developed about mid-Miocene and has existed in present condition from the late Miocene (Shackelton & Kenneth, 1975; Tankard et al., 1981). The aridity of western South Africa relates to upwelling of cold water of the Benguela Current and the origin of a cold Southern Ocean and thus could not have pre-dated the late Oligocene (Tankard et al., 1981).

In the Miocene, there was a pan-African vertebrate fauna in Namaqualand, there was a mosaic of sclerophyllus woodland, grassland, and scrub vegetation and summer rainfall that persisted throughout the late Tertiary. The earliest evidence of a modern semi-arid environment and winter rainfall in the southwestern Cape Province dates to the Pliocene (5 million years ago) (Tankard, 1978). Full semi-arid conditions with winter rainfall were achieved in western South Africa by the end of the Pliocene or early Pleistocene.

Progressive aridity stretched eastward. The short coastal rivers from the Orange River to Agulhas dry up for the most part during the dry season, or are reduced to very low flow. The effect on the estuarine section of the rivers is that currents and wind-driven waves heap sand across the openings of the rivers with the result that lagoon-like aborted estuaries are formed that range in salinity from freshwater (< 5‰) to 22 to 32‰ with some becoming hypersaline due to evaporation. How fresh the aborted estuary is depends on how impermeable the bar is to salt water. *Tomichia* is never found in the lagoon section of aborted estuaries while *Hydrobia* (Hydrobiidae) is common there.

In this century, the Agulhas region has been affected by eastward reaching aridity. In the summers of 1969 and 1970 certain large

lakes in the Agulhas region dried up for the first time in 50 years. Farmers stated that the winter rains filled the lakes which usually had water all year long. Zoetendalsvlei was dry throughout a six to seven year drought that ended about 1973–1974. During the period of drought there were pools of water in the river beds, but the vleis were dry, especially during summer.

It is evident that populations of *Tomichia* responded to increasing aridity in different ways depending on longitudinal gradients of aridity and general ecological setting. The changes were from freshwater-aquatic towards greater physiological tolerance to increased salinity, amphibious, and finally terrestrial modes of existence. The climatic changes were generally gradual with pulses of severe drought increasing from west to east. Changes in selective pressures would likewise be gradual with erratic events of extreme desiccation increasing from west to east.

What we see in Namaqualand today are two relict populations where water availability is so limited that the snails are virtually amphibious. Namaqualand at one time had innumerable streams with perennial water. These streams probably had *Tomichia*. Today, two springs represent the last vestige of these once widespread populations, and their continued existence is tenuous.

The coastal vleis and pans so common from Ysterfontein across the Cape Flats to Agulhas have probably had annual cycles of drying from the Pliocene onward, a period of about 5 million years during which *T. ventricosa* and *T. tristis* became adjusted to their current ecological situations.

As one passes from Cape Province through the Transkei to Natal Province one passes into a wetter and tropical zone. It is here that one finds amphibious *T. natalensis*. Presumably there was perennial water in Natal throughout the Cenozoic; it is not known what caused *T. natalensis* to become amphibious. It is probable that pulses of drought in this area caused this adaptation.

Pre-adaptation for an amphibious existence

No modern Triculinae are amphibious or terrestrial while some Pomatiopsinae have become amphibious or terrestrial in various places and at different times. Are there morphological character-states that pomatiopsine taxa have that are not shared by triculine taxa and that predate pomatiopsine taxa of amphibious life? The answer is yes. The broad foot that all pomatiopsines have is essential for the amphibious mode of existence. Another feature is the elongated spermathecal duct extending to the anterior end of the mantle cavity that surely would facilitate successful copulation and sperm transfer out of water.

There is evidence that genetically and physiologically at least some pomatiopsines are pre-adapted to survive under increased salinities and desiccation. This was evident during experiments comparing the perennially aquatic topotype population of *T. differens* with the Ysterfontein Vlei population of *T. ventricosa* for survival under different conditions of salinity and desiccation.

In all desiccation experiments 25 adult snails from each population were placed in 9 cm Petri dishes. There was a dry and humid set for each species. Filter paper was fitted inside the lid and kept moist to produce a humid chamber. Dry chambers had no filter paper. The filter paper was moistened only to the extent that snails would not move about in the chamber. One dry and one humid chamber were removed from each of the sets and flooded with water from that species' environment on days 7, 14, 30, 60, 120, 150. The percentage of snails living and dead was determined by observing them for movement over a 24 hour period following flooding. There were no replicates to permit an analysis of variance. The results shown in Table 10 clearly indicate the profound differences between species as one would predict. Humidity is an essential feature for prolonged survival out of water for both species. Although not as

TABLE 10. Percentage of each species of *Tomichia* surviving after different lengths of time in dry and humid chambers.

	Species			
	T. ventricosa		*T. differens*	
Days	humid	dry	humid	dry
7	96	100	96	28
14	96	100	92	4
30	96	92	76	0
60	92	60	60	0
90	96	28	40	0
120	88	16	0	0
150	96	8	0	0

TABLE 11. Percentage of each species surviving one month in water of different salinities (‰).

	Species		
	(Not oxygenated)		(Oxygenated)
Salinities	*T. ventricosa*	*T. differens*	*T. differens*
0	84	100	96
5	96	100	100
10	96	68	100
15	92	68	100
20	80	0	96
25	100	0	100
33	100	0	0
42	84	0	0
50	52	0	0

tolerant of desiccation as *T. ventricosa,* a significant percentage of *T. differens* can survive at least three months without water in humid areas. No Mekong River triculine can exist more than a week out of water.

In the salinity experiments a range of salinities was established using water from Ysterfontein Vlei (50‰) and DieKelders (0‰). Chambers with 5, 10, 15, 20, 25, 33, 42, and 50‰ were established. A number of snails were gradually acclimated to each salinity by slowly increasing or decreasing salinities every day. Finally 25 snails were placed in each of the eight containers. There were three sets; two sets were not aerated (one with *T. ventricosa,* one with *T. differens*), and one set aerated (with *T. differens*). *T. differens* normally lives in highly oxygenated environments. Algae were grown in the water for food and oxygen (under standing water conditions). The water was changed every 4 to 5 days and dead snails were removed daily to prevent fouling of the water. After 30 days the percentage of snails living was determined by noting activity over 24 hours. Results are shown in Table 11. Again, there is a profound difference between species as expected. Oxygenated water clearly improves survival of *T. differens* under high salinity stress but only up to 25‰. Snails could be acclimated to 33‰ salinity and be active for two weeks before withdrawing into their shells and dying within one month. With oxygenation *T. differens* can probably live for months at 15 to 20‰. The point to be made here is that *T. differens* shows considerable salinity and desiccation tolerances as a freshwater species and could probably be selected to live under conditions somewhat similar to those where one finds *T. ventricosa.*

Tempo and mode of pomatiopsine evolution

There has been no cladogenesis that one can detect in the southern continental pomatiopsines. The *Coxiella* radiation of Australia is small and parallels the ecological adjustments seen in *Tomichia ventricosa.* The seven modern species of *Tomichia* of South Africa seem to have evolved starting in the mid-Miocene to early Pliocene in response to progressive aridity spreading from west to east. There was no pronounced tectonism associated with opening of new ecological space and considerable morphological diversity as seen in Southeast Asia. What is seen is more of a gradual adjustment to changing climate over a period extending some 25 million years. This gradual adjustment has resulted in a few physiologically defined species that have few morphological differences among them.

There are insufficient data to know when, precisely, the modern *Tomichia* radiation began, i.e. the date of origin of that species from which the seven modern taxa evolved. *T. ventricosa* is found in the Pliocene and presumably this precursor was present in the mid-Miocene about 14 million years ago. If this date is used as a rough estimate for the origin of the modern *Tomichia* radiation, then $R = 0.139$. Even if an individual speciation event was rapid, the overall picture over a period of 2 to 14 million years indicates a gradual change contrasted with the Triculinae radiation. It is clear, in contrasting the Mekong River Triculinae with the South African Pomatiopsinae, that there are two distinctly different tempos of evolution.

The mode of speciation of South African Pomatiopsinae clearly differs from that of the Mekong River Triculinae. The difference is one of a physiological radiation with low morphological diversity versus a radiation involving pronounced morphological diversity and comparatively narrow range of physiological adjustment. While this is the major aspect of mode that I wish to stress, more should be said of that aspect of mode involving the paradigms of punctuated equlibrium and phyletic gradualism. As discussed above, the Mekong River Triculinae generally fit the conditions expected in the punctuated equilibrium mode of Gould & Eldredge (1977) and Stanley (1979). South African *Tomichia* fit the

gradualistic model only in so far that there is slight, gradual morphological change and if the species are defined in traditional terms of morphology and presumed reproductive isolation. However, the physiological radiation opens a new dimension for consideration in comparing paradigms. We do not know the extent to which the physiological changes may be punctuational in the sense discussed by Jones (1981) for *Drosophila.* Given the scenario of gradual climatic change and the absence of an adequate fossil record in South Africa documenting the presence of species of *Tomichia* other than that of *T. ventricosa,* one can only assume a gradual change in genetically controlled physiological tolerances.

The mode and tempo of pomatiopsine radiation in Asia is more similar to that of the Triculinae. The introduction of proto-*Oncomelania* from the Indian Plate to mainland Asia was followed by dispersal to Japan and North America. At the end of the Miocene, there was a modest adaptive radiation in Japan involving cladogenesis and speciation (Table 1) associated with Japanese tectonism at that time (Davis, 1979). There is considerable morphological divergence as well as ecological divergence (Davis, 1979, table 2). *Cecina* is marine intertidal; *Oncomelania minima* and *Pomatiopsis binneyi* are freshwater-aquatic, *Blanfordia* is terrestrial. Considering introduction into Asia at 12 or 10 million years ago, and the 16 modern species that have evolved (including the subspecies of *Oncomelania hupensis*), R = 0.23 or 0.28 My^{-1} for the Asian pomatiopsine radiation. This is a comparatively rapid rate considering any group of animals, one associated with tectonics and a series of morphological changes. Therefore, it is the tempo and mode of environmental change and the extent of ecological space and complexity that determines the tempos and modes of evolution; it is not a matter of genetic background.

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APPENDIX 1. Field data for species of *Tomichia* collected for this study. The numbers (e.g. D_1) correspond to sites marked in Figs. 7 and 8. Coded sequences such as D77-13 refer to field numbers (D = Davis; 77 = 1977; 13 = 13th collection in 1977).

T. differens

D_1 D77-13; type-locality; from rocks in stream flowing from cave at the base of the cliff in front of the hotel, Die

Kelders; Cape Prov.; 34° 33′ S.; 19° 22′ E. Davis, G. M. and Smits, J.; 19 Nov. 1977; salinity 2‰.

D_2 D78-83; headwaters of stream flowing into Soetendalsvlei via Southbos' farm, crosses track between Jacobsdam and Bergplass about 6.5 to 7.0 mi. west of Soetendalsvlei; Cape Prov.; 34° 43′ S.; 19° 51′ E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 2‰.

D_3 D78-70; small stream with sedges, Nuwejaarsrivier, 5 km. NW of Elands—drift, opposite Vogelvlei; Agulhas region, Cape Prov.; 34° 38′ S.; 19° 52′ E. Davis, G. M.; 17 Jan. 1978; salinity ?

D_4 D78-2; bridge crossing stream flowing into Soetendalsvlei, road from Agulhas to Elim, 2.5 km. NW of Soutbos' farm; Agulhas region, Cape Prov.; 34° 42′ S.; 19° 56′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 1 Jan. 1978; salinity 2‰.

D78-78; same as D78-2; stream dried up, snails alive under stones, rocks. Davis, G. M. and Dichmont, T.; 19 Jan. 1978.

D_5 D78-71; on sedges in Nuwejaarsrivier, before entering Soetendalsvlei, opposite Soutbos' farm; Agulhas region, Cape Prov.; 34° 43′ S.; 19° 57′ E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.

D_6 D78-73; in Nuwejaarsrivier and vlei next to the river at opening of river into Soetendalsvlei; Agulhas region, Cape Prov.; 34° 44′ S.; 19° 58′ E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.

D_7 D78-79; on rocks and water plants in Nuwejaarsrivier below the vlei, where road from Agulhas forks to Elim and Bredarsdorp. In sympatry with *Gyraulus* sp.; Agulhas region, Cape Prov.; 34° 41′ S.; 19° 55′ E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 0‰.

D_8 D78-62; on grass, sticks, mud at stream margins of Karsrivier, about 2 mi. SW of Bredarsdorp-Arniston road; Cape Prov.; 34° 35′ S.; 20° 00′ E. Davis, G. M. and Dichmont, T.; 16 Jan.1978; salinity 0‰

D_9 D78-6; on grass in roadside pool, pool about 70′ long × 20′ wide, ankle deep, road from Malgas to Heidelberg, 20 km. from Heidelberg; Cape Prov.; 34° 11′ S.; 20° 46′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 3‰.

D_{10} D78-7; small streams alongside road from Malgas to Heidelberg, 18 km. from Heidelberg, Karringmelksrivier drainage; Cape Prov.; 34° 09′ S.; 20° 48′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 3‰.

D_{11} D78-8; large stream, Slangrivier, where road from Malgas to Heidelberg crosses, about 8 km. from Heidelberg. Snails common on algal mats; Cape Prov.; 34° 08′ S.; 20° 52′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 9.5‰.

D_{12} D78-55A; stream to E of road from Riversdale to Stillbaai, Riversdale area, 4 km. N of Stillbaai, stream flows into Kafferkuilsrivier. Snails numerous on the algae; Cape Prov.; 34° 19′ S.; 21° 24′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 8 Jan. 1978; salinity 4‰.

T. natalensis

N_1 D78-208; snails amphibious on mud stream banks, Inyezane River, 2 km. from Gingindlovu where back road from Gingindlovu to the shrimp farm crosses the river; Zululand, Natal Prov.; 29° 03′ S.; 31° 37′ E. Davis, G. M.; 4 Sept. 1978; salinity 0‰.

N_2 D78-207; snails amphibious, distributed on damp mud slopes of Inyezane River, under old reed stems in shaded areas. Where highway N_2 from Gingindlovu to Empangani crosses the stream, some 6 km. NE of Gingindlovu; Zululand, Natal Prov.; 28° 59′ S.; 31° 39′ E. Davis, G. M.; 4 Sept. 1978; salinity 0‰.

N_3 D78-212; snails numerous on mud, stacks of reeds, amphibious. Imbati River where highway N_2 crosses between Emoyeni and Mtunzini; Zululand, Natal Prov.; 28° 57′ S.; 31° 42′ E. Davis, G. M.; 5 Sept. 1978; salinity 0‰.

N_4 D78-213; snails amphibious on banks of Ubati River at N_2 road crossing between D78-212 and Mtunzini turn-off; Zululand, Natal Prov.; 28° 57′ S.; 31° 43′ E. Davis, G. M.; 5 Sept. 1978; salinity 0‰.

T. rogersi

R_1 D77-20; type-locality; stream opposite schoolhouse, Eksteenfontein. Eksteenfontein = Stinkfontein (name changed from meaning stinking spring to no longer stinking spring). Beginning of Stinkfontein River flowing to the Orange River; Namaqualand; 28° 50′ S.; 17° 14′ E. Davis, G. M. and Smits, J.; 29 Nov. 1978; salinity 5‰.

R_2 D77-19; seepage from small capped (windmill) spring, Lekkersing; Namaqualand; 29° 01′ S.; 17° 6′ E. Davis, G. M., Whitehead, V. and Smits, J.; 29 Nov. 1977; salinity 4‰.

T. tristis

T D78-53; snails amphibious, high shoreline under branches, logs, with *Assiminea* sp., soil dark black loam. W side of Seekoeirivier, lagoon at upper end of the lagoon near Aston, Bay Beach; Cape Prov.; 34° 05′ S.; 24° 53′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 6 Jan. 1978; salinity in lagoon 20‰.

T. ventricosa

V_1 D77-11; snails clustered on rocks in vlei, Ysterfontein; Cape Prov.; 33° 20′ S.; 18° 10′ E. Davis, G. M.; 15 Nov. 1977; salinity 12‰.

D77-51; 30 Dec. 1977; salinity 28‰.

D78-88; 4 Feb. 1978; salinity 58‰ at center of vlei; 83‰ in shallows.

V_2 D78-86; dead shells collected on northern shore, Rietvlei, Milnerton; Cape Prov.; 33° 50′ S.; 18° 32′ E. Davis, G. M.; 28 Jan. 1978; salinity 8‰.

V_3 D77-44A; all dead shells in vlei, vlei three quarters of the way from sewage plant to Chapmans Bay, Wild Bird Vlei; Cape Peninsula, Cape Prov.; 34° 08′ S.; 18° 21′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 29 Dec. 1977; salinity 158‰.

D77-44B; all dead shells in vlei, vlei at point where water goes subterranean near Chapmans Bay; salinity 40‰.

D77-44C; vlei half way between sewage plant and Chapmans Bay; salinity 160‰.

V_4 D77-27; Quaternary fossils collected in central area, Sandvlei, Ladeside near Muizenberg; Cape Prov.; 34°05′ S.; 18° 28′ E. Davis, G. M. and Smits, J.; 6 Dec. 1977; salinity 2‰.

D77-28; same as D77-27, collected from main lake, no live snails; salinity 4‰.

D77-29; in masses of green algae in small pool to west of small dirt road that runs between vlei and railroad tracks, above Marina Dagama, Muizenberg; Cape Prov.; 34° 06′ S.; 18° 28′ E. Davis, G. M. and Smits, J.; 6 Dec. 1977; salinity 10‰.

D77-50; snails on underside of floating algal masses, Sandvlei, Muizenberg; Cape Prov.; 34° 06′ S.; 18° 28′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 29 Dec. 1977; salinity 8‰.

V_5 D77-39; turn off N_2 at first Kuilsrivier exit from Cape Town, bridge over Kuilsrivier, up stream ½ mile. No live snails; Cape Prov.; 34° 01′ S.; 18° 39′ E. Davis, G. M. and Hoagland, K. E.; 28 Dec. 1977; salinity 3‰.

V_6 D78-87A,B; Bermont, Vermont vlei next to road between Hawston and Onrus. Vlei had dried up completely; Cape Prov.; 34° 25′ S.; 19° 10′ E. Davis, G. M. and Whitehead, V.; 29 Jan. 1978; salinity 60‰.

V_7 D77-16; just before Kleinriviersvlei widens into Hermanus Lagoon, W of Stanford between Stanford and Wortelgat; Cape Prov.; 34° 27′ S.; 19° 25′ E. Davis, G. M. and Smits, J.; 20 Nov. 1977; salinity 4‰.

V_8 D77-17; Kleinriviers; dead snails under masses of algae; Cape Prov.; 34° 25′ S.; 19° 19′ E. Davis, G. M. and Smits, J.; 20 Nov. 1977; salinity 22‰.

V_9 D77-14; dead shells ¾ mile up Boemans River from bridge at shore, Franskraal; Cape Prov.; 34° 35′ S.;

19° 24′ E. Davis, G. M. and Smits, J.; 19 Nov. 1977; salinity 19‰.

V_{10} D78-67; vlei 4 km. NW of Wiesdrift; Agulhas Region, Cape Prov.; 34° 40′ S.; 19° 54′ E. Davis, G. M.; 17 Jan. 1978; salinity 10‰.

V_{11} D78-69; small, shallow vlei between Waskraals vlei and Voëlvlei; Agulhas region, Cape Prov.; 34° 39′ S.; 19° 51′ E. Davis, G. M.; 17 Jan. 1978; salinity ?

V_{12} D78-82; small vlei between Vitkyk and Bergplaas farms, just N of Soetanysberg, 6 mi W of middle of Soetendalsvlei; Cape Prov.; 34° 42′ S.; 19° 53′ E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity ?

V_{13} D78-81; small vlei in nature reserve on N side of road from Rhenosterkop to Asfontein, on S side of Soetendalsvlei; Cape Prov.; 34° 46′ S.; 19° 54′ E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity ?

V_{14} D78-75A; W side of road from Soetendalsvlei to Springfield, crosses stream flowing to salt pan; Cape Prov.; 34° 44′ S.; 19° 55′ E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 25‰.

D78-75B; dried, twisting channel to salt pan on E side of road, snails under dried algae mats and rocks; salinity ?

V_{15} D78-80; pan at Rhenosterkop, 4 mi W of S end of Soetendalsvlei. Snails numerous on sand and clustered on stones; Cape Prov.; 34° 46′ S.; 19° 56′ E. Davis, G. M. and Dichmont, T.; 19 Jan. 1978; salinity 32‰.

V_{16} D78-64; Rondepan, large vlei on S side of road from Bredarsdorp to Elim, 14 km. from Bredarsdorp. Snails under stones; Cape Prov.; 34° 37′ S.; 19° 56′ E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 20‰.

V_{17} D78-65A; Langepan, main part of vlei. On road from Bredarsdorp to Elim, 16 km. from Bredarsdorp. Snails on sedges and sandy bottom; Cape. Prov.; 34° 37′ S.; 19° 54′ E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 8‰.

V_{18} D78-38; Kowie River, Port Alfred; Cape Prov.; 33° 36′ S.; 26° 53′ E. Davis, G. M. and Hoagland, K. E.; 5 Jan. 1978; salinity 32‰.

T. zwellendamensis

Z_1 D78-68; Waskraalsvlei, snails on stems of sedges; Agulhas region, Cape Prov.; 34° 40′ S.; 19° 50′ E. Davis, G. M.; 17 Jan. 1978; salinity 0‰.

Z_2 D78-74; large circular vlei in the Nuwejaarsrivier, about 1 km. W of Soetendalsvlei. Snails numerous on marl bottom and on sedges; Cape Prov.; 34° 43′ S.; 19° 58′ E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity ?

Z_3 D78-73A; vlei next to the Nuwejaarsrivier at opening of river into Soetendalsvlei; Agulhas region, Cape Prov.; 34° 44′ S.; 19° 58′ E. Davis, G. M. and Dichmont, T.; 18 Jan. 1978; salinity 0‰.

D78-73B; in Nuwejaarsrivier opposite vlei; salinity 0‰.

Z_4 D78-65B; Langepan, where vlei exits along road flowing to the east. On road from Bredarsdorp to Elim, 16 km. from Bredarsdorp. Snails in reeds; Cape Prov.; 34° 37′ S.; 19° 54′ E. Davis, G. M. and Dichmont, T.; 16 Jan. 1978; salinity 8‰.

Z_5 D78-4; De Hoopvlei on road from Skipskop to Potbergsrivier. Snails on sand, rocks, stems of grass and algae; Cape Prov.; 34° 29′ S.; 20° 26′ E. Davis, G. M., Hoagland, K. E. and Smits, J.; 2 Jan. 1978; salinity 5‰.

APPENDIX 2. Systematics.

Tomichia ventricosa: type-species

Introduction—Anatomical data presented for *T. ventricosa* serve to define the genus as well as the species. The only data discussed for other species are those demonstrating differences among species. The anatomy of *Tomichia ventricosa* clearly indicates that this genus belongs to the Pomatiopsidae: Pomatiopsinae as defined by Davis (1967,

TABLE 12. Shell measurements (mm) of species of *Tomichia* from specimens used for anatomical studies yielding data in Tables 13–28. Mean ± standard deviation; (range). N = 5 unless otherwise indicated.

Species	Length	Length of body whorl	Width	Length of aperture	Width of aperture
T. differens					
Females; 6.0–6.5 whorls	4.66 ± 0.14 (4.44 – 4.80)	3.12 ± 0.14 (2.92 – 3.28)	2.48 ± 0.13 (2.36 – 2.69) N = 4	2.14 ± 0.12 (2.0 – 2.28) N = 4	1.38 ± 0.12 (1.32 – 1.55) N = 4
Males; 6.0–6.5 whorls	4.92 ± 0.36 (4.32 – 5.28)	3.06 ± 0.16 (2.8 – 3.2)	2.48 ± 0.12 (2.4 – 2.6)	2.10 ± 0.12 (1.92 – 2.28)	1.34 ± 0.06 (1.28 – 1.40)
T. natalensis					
Females; 6.0–6.5 whorls	4.99 ± 0.12 (4.88 – 5.12)	2.98 ± 0.04 (2.92 – 3.0)	2.48 ± 0.06 (2.40 – 2.50)	1.99 ± 0.06 (1.92 – 2.08)	1.49 ± 0.05 (1.4 – 1.52)
Males; 6 whorls	4.50 ± 0.19 (4.4 – 4.8)	2.74 ± 0.10 (2.68 – 2.88)	2.24 ± 0.07 (2.16 – 2.32)	1.86 ± 0.10 (1.72 – 2.0)	1.30 ± 0.04 (1.28 – 1.36)
T. rogersi					
Females; 6.5–7.0 whorls	7.74 ± 0.23 (7.44 – 7.92) N = 4	4.47 ± 0.15 (4.64 – 4.92)	3.54 ± 0.17 (3.28 – 3.76)	2.92 ± 0.13 (2.76 – 3.04) N = 4	2.08 ± 0.06 (2.04 – 2.16) N = 4
Males; 7.0–7.5 whorls	8.6 ± 0.26 (8.2 – 8.84)	5.02 ± 0.09 (4.88 – 5.12)	3.85 ± 0.14 (3.72 – 4.00)	2.99 ± 0.14 (2.83 – 3.20)	2.22 ± 0.07 (1.08 – 2.32)
T. tristis					
Mixed males and females; eroded apices N = 7	7.15 ± 0.67 (6.08 – 8.08)	4.0 ± 0.10 (3.84 – 4.12)	3.30 ± 0.11 (3.2 – 3.48)	2.52 ± 0.14 (2.32 – 2.71)	1.76 ± 0.07 (1.72 – 1.88)
T. ventricosa					
Females; 3 whorls (eroded)	5.43 ± 0.43 (5.08 – 6.08)	3.46 ± 0.37 (2.88 – 3.76)	2.63 ± 0.14 (2.48 – 2.84)	2.18 ± 0.23 (2.00 – 2.52)	1.44 ± 0.16 (1.32 – 1.72)
Males	4.4 ± 0.38 (3.88 – 4.92)	2.90 ± 0.29 (2.52 – 3.32)	2.09 ± 0.21 (1.92 – 2.36) N = 4	1.76 ± 0.18 (1.52 – 2.00)	1.16 ± 0.10 (1.04 – 1.28)
T. zwellendamensis					
Females; 7.5–8 whorls N = 4	5.41 ± 0.32 (5.0 – 5.68)	2.71 ± 0.18 (2.52 – 2.88)	2.14 ± 0.19 (1.88 – 2.32)	1.78 ± 0.12 (1.60 – 1.84)	1.18 ± 0.16 (0.96 – 1.36)
Males; 7.5–8 whorls	5.47 ± 0.20 (5.20 – 5.72)	2.60 ± 0.12 (2.40 – 2.68)	2.08 ± 0.13 (1.96 – 2.24)	1.70 ± 0.07 (1.60 – 1.76)	1.18 ± 0.08 (1.08 – 1.36)

1968, 1979). Characters and character states serving to define family and subfamily categories are not discussed here.

Shells (Figs. 7, 8)—Shells of mature adults of the Ysterfontein population (Appendix 1, V_1) are invariably eroded, three to five whorls but mostly three whorls. Statistics of shell measurements are given in Table 12. The length of the last three whorls is 5.46 ± 0.34 mm (Fig. 12). Shape is turreted (Figs. 7, 8). Whorls moderately convex, sutures correspondingly moderately impressed. Color light brown to brown-yellow; shell glistening. Aperture ovate (Fig. 13) lips moderately thick; peristome complete with well-developed parietal callus. Inner lip reflected from parietal callus to abapical end of aperture; reflection over umbilical and basal region of body whorl. Reflection of lip at abapical end creates nearly spout-like appearance. Due to reflection of inner lip, broad arc of columella exposed inside aperture.

Umbilicus varies from chink to widely open. Shells mostly smooth (12×); some with pronounced irregular growth lines. Spiral microlines on some whorls of a few shells. Outer lip with little or no sinuation (side view).

Shell of adults from Kleinrivier (Appendix 1, V_8) differ from those discussed above as follows: all shells with eroded apices, two or three whorls remaining. Color, dull brown due to thick periostracum; thus shell not glistening.

TABLE 13. Length dimensions (mm) or number of non-neural organs of *Tomichia ventricosa*.

	No.	$\bar{X}$	Sd	Range
Organ (♀)				
Body	5	8.70	0.64	7.6–9.2
Buccal mass	5	1.03	0.17	1.40–3.40
Anterior pallial oviduct	4	2.30	0.82	1.40–3.40
Posterior pallial oviduct	4	1.80	0.49	1.20–2.40
Total pallial oviduct (Po)	4	4.10	0.75	3.80–5.20
Bursa copulatrix (Bc)	5	1.18	0.15	1.00–1.40
Bc/Po	4	0.31	0.07	0.23–0.40
Seminal receptacle	5	0.16	0.03	0.14–0.20
Digestive gland	5	2.98	0.60	2.20–3.60
Gonad	4	1.23	0.33	0.90–1.60
Mantle cavity	4	2.87	0.43	2.60–3.50
Ctenidium	4	2.43	0.40	2.10–3.00
Gill filaments (no.)	5	55.4	1.67	54–58
Organ (♂)				
Body	5	7.02	1.31	5.8 –8.6
Prostate	5	1.07	0.20	0.76–1.30
Digestive gland	5	3.18	0.55	2.60–3.90
Gonad	5	3.06	0.50	2.60–3.90
Seminal vesicle	4	1.60	0.49	1.0 –2.20
Penis	5	1.63	0.39	1.20–2.10
Mantle cavity	5	2.34	0.24	2.00–2.60
Ctenidium	5	2.10	0.15	1.94–2.30
Gill filaments (no.)	5	39.8	2.28	36–42

Aperture an elongate oval (Fig. 13), lips thin, outer lip very fragile. Parietal callus dips slightly into and filling umbilicus of most shells. Inner lip slightly reflected; columellar arc inside aperture not pronounced and narrows to thin strip about mid-parietal callus.

Umbilicus lacking; <5% have chink. Shells with regular discernable growth lines (12×). Length of last three whorls 5.30 ± 0.48 mm (Fig. 12).

Organ measurements—See Table 13 for measurements, counts, or ratios involving non-neural organs or structures; Table 14 for statistics on neural structures.

External features—The head (Fig. 14) is densely pigmented except for the tip of the snout (Sn). Scattered white glandular units (Gl) are concentrated around the eyes (Ey) and extend a short distance out along the

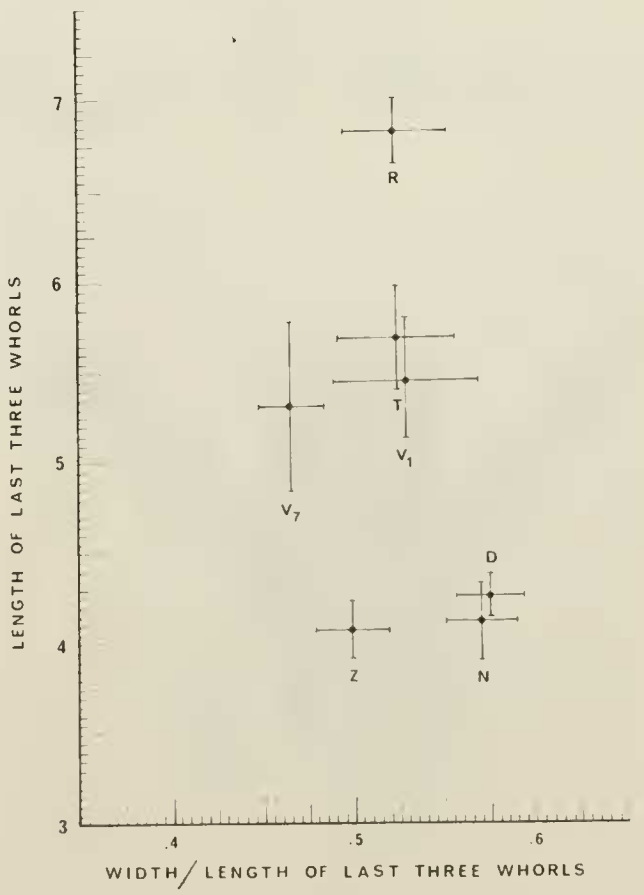

FIG. 12. Mean and standard deviation for length of last three whorls (mm) plotted against the ratio width: length of last three whorls. D, *Tomichia differens* (topotypes); N, *T. natalensis*; R, *T. rogersi* (topotypes); T, *T. tristis*; V, *T. ventricosa*; Z, *T. zwellendamensis*.

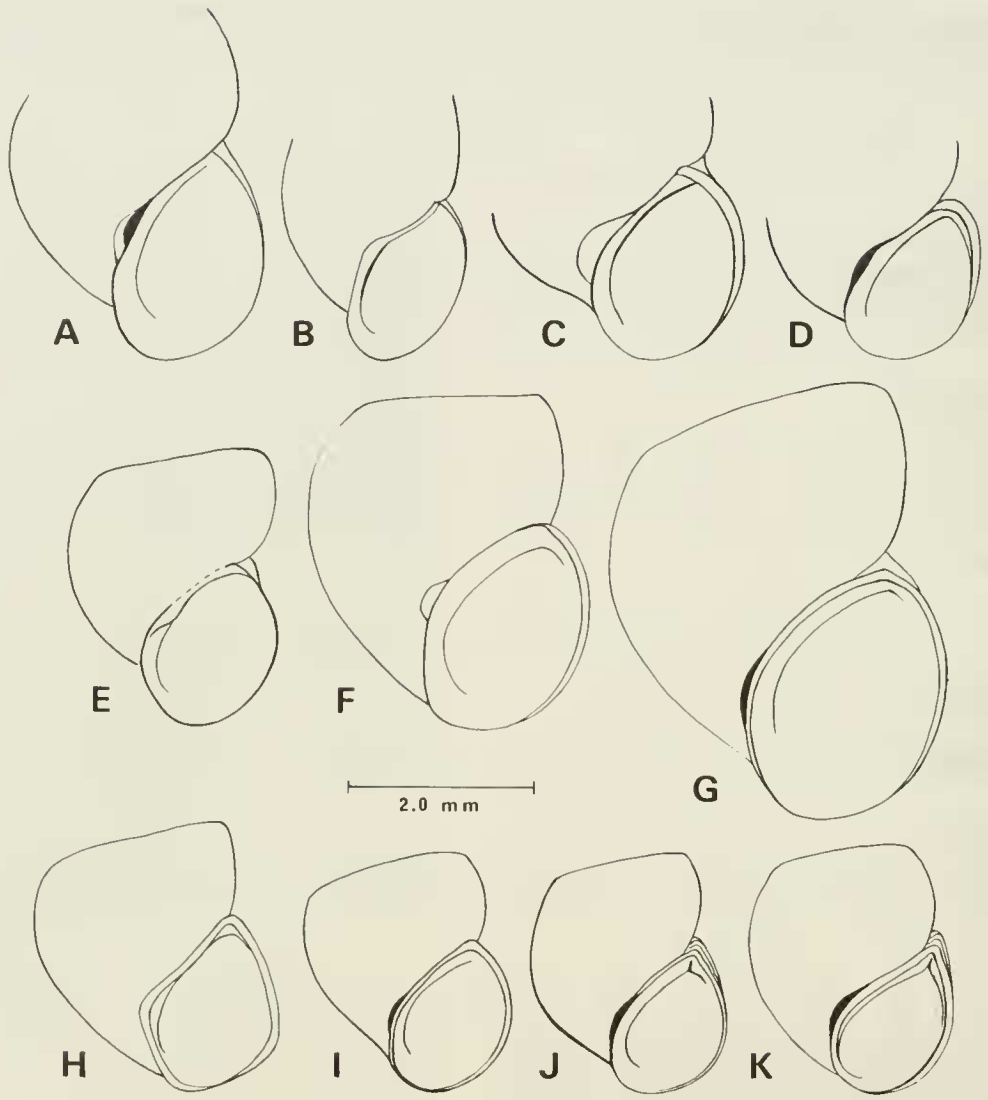

FIG. 13. A demonstration of differences among taxa in aperture shape. A, B, *Tomichia ventricosa* (D77-16); C, D, *T. ventricosa* (D77-51); E, *T. zwellendamensis* (Note fold on columella); F, *T. tristis*; G, *T. rogersi* (topotypes); H, I, *T. natalensis*; J, K, *T. differens* (topotype).

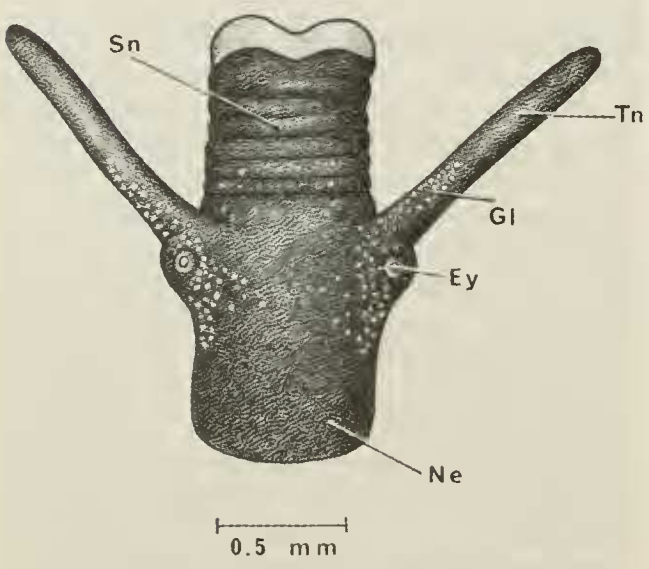

FIG. 14. The head of *Tomichia ventricosa*. Ey, eye; Gl, white glandular units; Ne, neck; Sn, snout; Tn, tentacle.

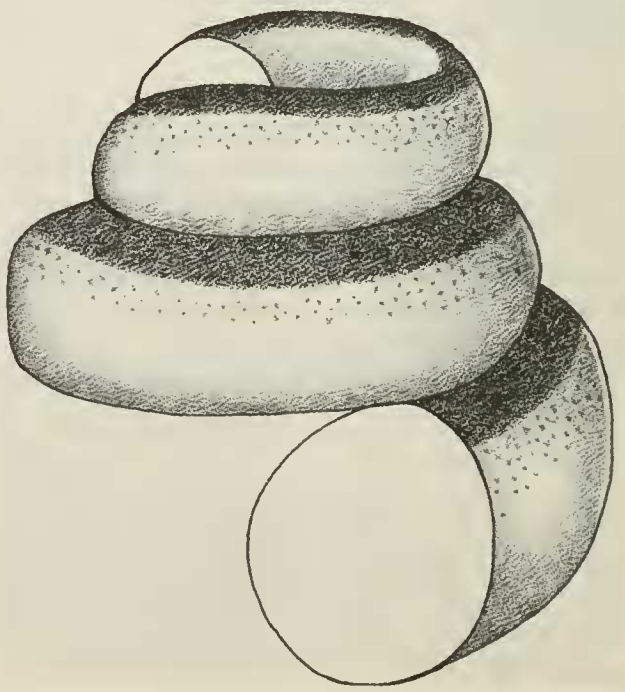

FIG. 15. Body whorls of *T. ventricosa* demonstrating dorsal strip of dense melanin pigment.

TABLE 14. Measurements (mm) of lengths of neural structures from female *Tomichia ventricosa*.

Structure	No.	$\bar{X}$	Sd	Range
Cerebral ganglion	5	0.32	0.03	0.28–0.36
Cerebral commissure	5	0.25	0.03	0.20–0.28
Pleural ganglion—right (1)	5	0.18	0.03	0.16–0.22
—left	5	0.15	0.04	0.10–0.20
Pleuro-supraesophageal connective (2)	5	0.42	0.09	0.30–0.50
Supraesophageal ganglion (3)	5	0.17	0.02	0.16–0.20
Osphradiomantle nerve	2	0.12	—	0.10–0.14
Pleuro-subesophageal connective	5	0.04	0.05	0.02–0.14
Subesophageal ganglion	5	0.14	0.02	0.12–0.16
Pedal ganglion	4	0.26	0.04	0.20–0.30
Pedal commissure	5	0.07	0.03	0.04–0.10
Statocyst (diameter)	5	0.11	0.01	0.10–0.12
Osphradial ganglion	4	0.48	0.07	0.40–0.56
Visceral ganglion	5	0.21	0.02	0.18–0.24
RPG ratio	5	0.54	0.04	0.48–0.59

tentacles (Tn). The dorsal aspect of the whorls of the body have a dense pigment band (Fig. 15).

Digestive system—Radular data are given in Tables 15–17. SEM pictures of the radula are given (Fig. 10). The radula is typically pomatiopsid. The tip of the radular sac (Fig. 16, Trs) is directly beneath the central posterior aspect of the buccal mass.

Female reproductive system (Figs. 17–20)—The uncoiled female is shown without head and kidney tissue revealing the standard pomatiopsine ground plan (Fig. 17). Cutting across the mantle cavity and removing connective tissues from the bursa copulatrix reveals organs as shown in Fig. 18. One clearly sees the opening of the kidney (Oki) projecting into the rear of the mantle cavity. The bursa copulatrix (Bu) is shown in the same relationship to the pallial oviduct (Ppo) as in Fig. 17. The bursa is extremely long, 31% the length of the pallial oviduct (Table 13). The anterior tip of the bursa (Tbu) extends into the cavity of the kidney anterior to that point where the oviduct passes into the posterior pallial oviduct (= albumen gland) (Opo). The tip of the bursa is within the narrowing funnel of the kidney just before the kidney opens into the mantle cavity.

The bursa copulatrix complex shown in Figs. 19, 20 is in the same position as shown in Figs. 17, 18. The interrelationships of the

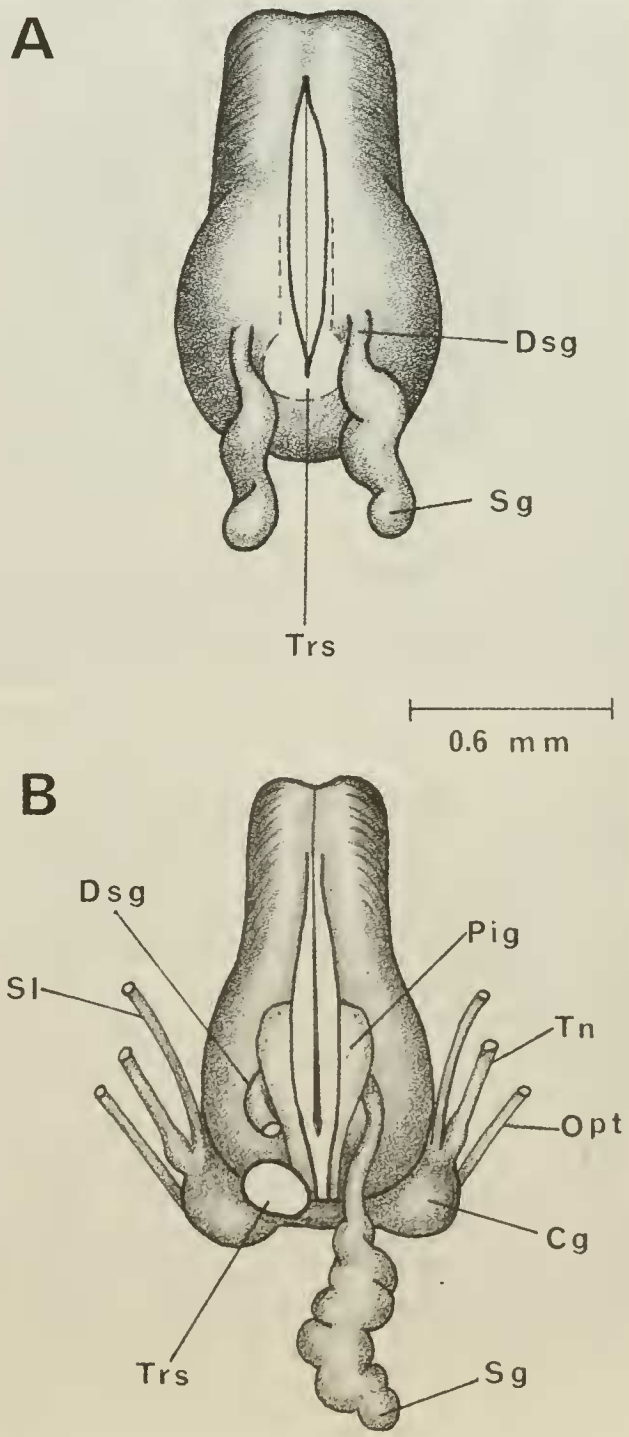

FIG. 16. Dorsal buccal mass of A, *T. ventricosa* and B, *T. differens*. Cg, cerebral ganglion; Dsg, duct of salivary gland; Opt, optic nerve; Pig, pigmented region on dorsal buccal mass; Sg, salivary gland; Sl, supralabial nerve; Tn, tentacular nerve; Trs, tip of radular sac.

TABLE 15. Radular statistics. Mean ± standard deviation; (range). Measurements in mm. No. = number of radulae studied unless otherwise stated as N =.

Taxon	Population: see Appendix 1	No.	Radula length	Radula width	No. rows teeth	No. rows forming	Central tooth width	Length of radula ÷ length of buccal mass
T. differens	D_1	17	1.28 ± 0.07 (1.16 – 1.38)	0.17 ± 0.01 (0.16 – 0.18)	70.5 ± 3.8 (65 – 76)	10.5 ± 1.1 (5 – 26) N = 16	0.042 ± 0.001 (0.04 – 0.043) N = 5	1.26
	D_{11}	3	0.87 ± 0.09 (0.79 – 0.97)	0.13 ± 0 (0.13)	64.7 ± 6.5 (58 – 71)	6.7 ± 0.6 (6 – 7)	0.030 ± 0 (0.03)	—
	D_{12}	9	1.21 ± 0.11 (1.12 – 1.34)	—	93.3 ± 4.7 (86 – 100)	12.7 ± 3.2 (7–17)	0.031 ± 0.002 (0.028 – 0.033)	1.19
	D_4	3	1.16 ± 0.08 (1.09 – 1.23)	0.15 ± 0 (0.15)	83.0 ± 2.0 (81 – 85)	7 ± 0 (7)	0.032 ± 0.001 (0.03 – 0.033)	—
T. natalensis	N_3	9	0.91 ± 0.05 (0.85 – 0.97)	0.12 ± 0.01 (0.11 – 0.13)	71.2 ± 5.0 (63 – 78)	6.1 ± 0.8 (5 – 7)	0.027 ± 0.003 (0.023 – 0.031)	0.98
T. rogersi	R_1	4	1.39 ± 0.04 (1.36 – 1.43)	0.18 ± 0.01 (0.17 – 0.19)	72.0 ± 3.2 (68 – 75)	5.8 ± 0.5 (5 – 6)	0.043 ± 0.002 (0.041 – 0.045)	1.07
	R_2	9	—	—	—	—	0.041 ± 0.002 (0.037 – 0.043)	—
T. tristis	T	8	1.23 ± 0.09 (1.12 – 1.40)	0.15 (0.14 – 0.16) N = 2	77.6 ± 6.5 (69 – 87)	5.3 ± 1.5 (4 – 8)	0.035 ± 0.001 (0.034 – 0.036)	0.95
T. ventricosa	V_1	2	—	—	—	—	0.040 ± 0.001 (0.039 – 0.041)	—
	V_7	14	1.10 ± 0.09 (0.96 – 1.21)	0.15 ± 0.01 (0.13 – 0.16)	72.1 ± 3.6 (67 – 79)	6.8 ± 0.98 (6 – 9)	0.038 ± 0.002 (0.035 – 0.041)	1.06
	V_4	5	1.14 ± 0.07 (1.06 – 1.22)	— —	69.6 ± 3.2 (65 – 74)	11.0 ± 1.0 (10 – 12)	0.035 ± 0.001 (0.034 – 0.036)	—
	V_{18}	3	0.78 ± 0.07 (0.70 – 0.82)	0.12 ± 0 (0.12)	60.6 ± 3.0 (57 – 63)	4.7 ± 0.6 (4 – 5)	0.028 ± 0.003 (0.025 – .030)	—
(+ *producta*)	V_{15}	8	1.20 ± 0.11 (1.07 – 1.36)	0.16 ± 0.01 (0.15 – 0.17)	59.0 ± 7.3 (51 – 66)	5.1 ± 0.4 (5 – 6)	0.041 ± 0.003 (0.038 – 0.045)	—
T. zwellendamensis	Z	8	0.93 ± 0.07 (0.89 – 1.04)	0.13 ± 0.004 (0.13 – 0.14)	65.3 ± 5.1 (59 – 73)	5.9 ± 0.6 (5 – 7)	0.039 ± 0.004 (0.035 – 0.045)	1.08

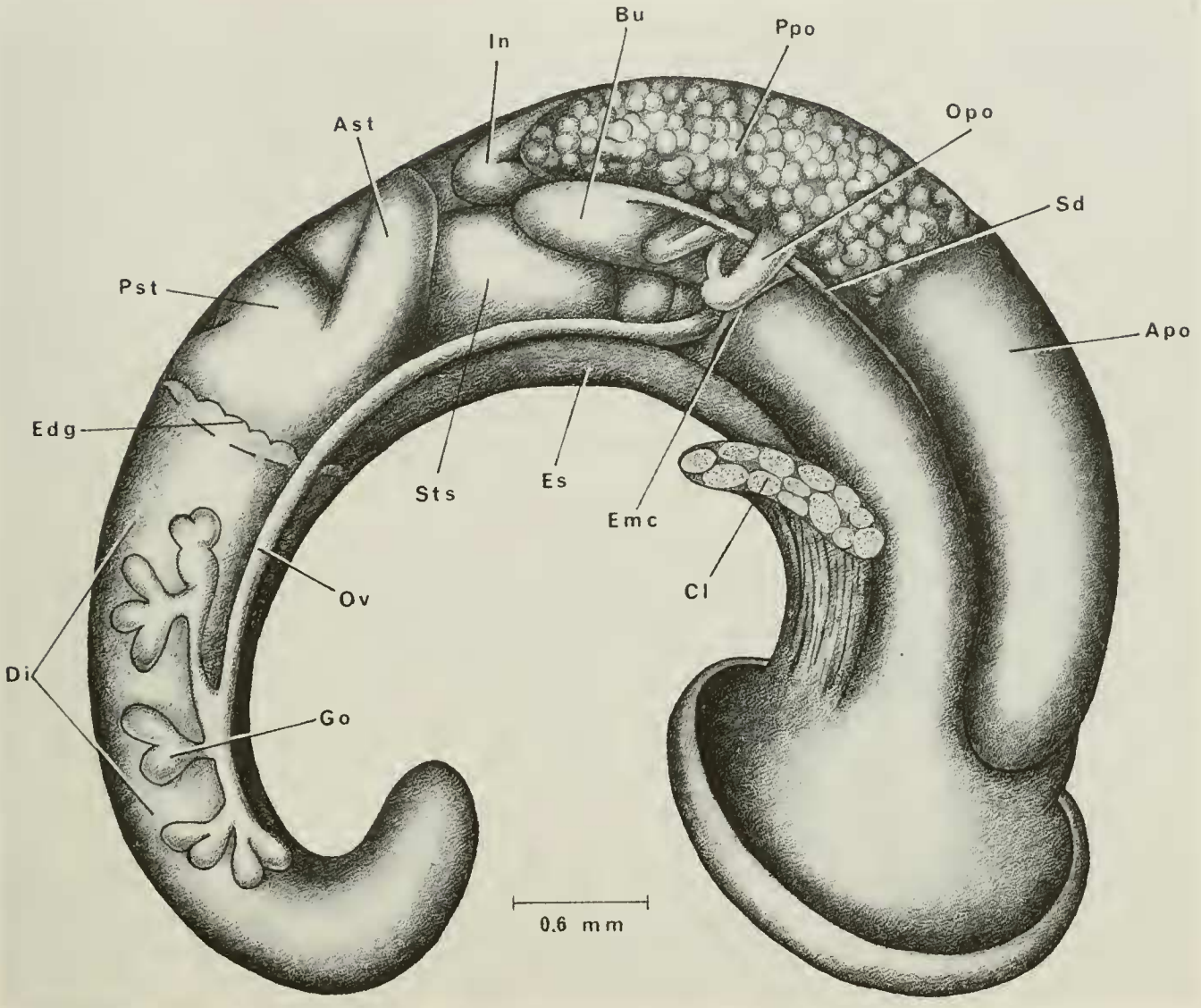

FIG. 17. Female *T. ventricosa,* uncoiled, with head and kidney tissue removed. Apo, anterior pallial oviduct (= capsule gland); Ast, anterior chamber of stomach; Bu, bursa copulatrix; Cl, columellar muscle; Di, digestive gland; Edg, anterior end of digestive gland; Emc, posterior end of mantle cavity; Es, esophagus; Go, gonad; In, intestine; Opo, opening to oviduct into posterior pallial oviduct (albumen gland); Ov, oviduct; Ppo, posterior pallial oviduct (= albumen gland); Pst, posterior chamber of stomach; Sd, spermathecal duct; Sts, style sac.

spermathecal duct (Sd), sperm duct (Sdu), seminal receptacle (Sr), oviduct (Ov), and bursa are shown. In Fig. 19A, from a different individual, the bursa was rotated slightly and the oviduct at the opening to the pallial oviduct (Opo) pulled through an arc of 90° toward the observer from its position shown in Figs. 18, 19B to clearly show the position of the seminal receptacle, the nature of the coils of the sperm duct and oviduct. Note that the oviduct is densely pigmented between the point where the sperm duct connects and the opening into the pallial oviduct (Fig. 19A, Pig).

My figure of the bursa complex (Davis 1979, fig. 9) is in error as it shows the sperm duct (Sdu) connecting the oviduct to the spermathecal duct as in *Pomatiopsis,* and as it shows the seminal receptacle dorsal to the bursa as in *Pomatiopsis.* This figure was from dissections of two individuals in 1964 when I was dissecting *Pomatiopsis lapidaria.* In fact the sperm duct arises from the bursa copulatrix close to, and anterior to the point where the spermathecal duct enters the bursa. The seminal receptacle tucks between the coils of the sperm duct and the bursa on the ventral surface of the bursa.

The opening (Op) of the pallial oviduct (Apo) is shown together with the opening of the spermathecal duct (Osp) (Fig. 19C). These openings are at the anterior end of the mantle cavity. The pallial oviduct produces a

TABLE 16. Cusp formula for populations of South African *Tomichia*. ( )* = % radulae with the formula if other than 100%.

Taxon	Populations: See Appendix 1	No.	Central tooth	Lateral tooth	Inner marginal	Outer marginal
T. differens	D_1	5	$\frac{2-1-2}{2-2}$ (80)*	3 – 1 – 3 (90)*	9 – 10	9 – 10
			$\frac{1-1-1}{2-2}$ (20)*	3 – 1 – 4 (10)*		
	D_4	3	$\frac{2-1-2}{2-2}$	3 — 1 — 3	10 – 11	9 – 10
	D_{12}	9	$\frac{2-1-2}{3-3}$ (78)*	3 – 1 – 3(4) (44)*	12 – 13	11
			$\frac{2-1-2}{2-2}$ (22)*	3 – 1 – 3 (56)*		
	D_{14}	3	$\frac{2-1-2}{2-2}$	3 – 1 – 3	10	8 – 9
T. natalensis	N_3	5	$\frac{2-1-2}{3-3}$	2(3) – 1 – 3	8 – 9	8 – 10
T. rogersi	R_1	9	$\frac{2-1-2}{3-3}$ (89)*	2 – 1 – 3(4) (89)*	10 – 12	8 – 10
			$\frac{2-1-2}{2-2}$ (11)*	2 – 1 – 3 (11)*		

	R_2	9	$\frac{2-1-2}{2-2}$ (43)* $\frac{3-1-3}{2-2}$ (57)*	2 – 1 – (4)3 (89)* 2 – 1 – 3 (11)*	11 – 12 (71)* 12 — 13 (29)*	9 – 10
T. tristis	T	6	$\frac{2-1-2}{2-2}$	3 – 1 – (4)3 (33)* 3 – 1 – (2)3 (33)* 3 – 1 – 3 (33)*	11 – 12	9 – 10
T. ventricosa	V_1	2	$\frac{2-1-2}{3-3}$	3 – 1 – 3	14 – 15	9 – 10
	V_7	9	$\frac{2-1-2}{2-2}$ (33.3)* $\frac{2-1-2}{3(2)-3}$ (22.2)* $\frac{2-1-2}{3-3}$ (44.4)*	3 – 1 – 3(4)	10 (3.3)* 11 (9.0)* 14 (13.3)* 12 – 13 (74.4)*	8 – 11 (on one radula 11 on left side 9 on right side)
	V_4	5	$\frac{2-1-2}{3-3}$	3 – 1 – 3 (80)* 3 – 1 – (4)3 (20)*	13 – 14	10 – 11
	V_{18}	3	$\frac{2-1-2}{3-3}$	3 – 1 – 3	14 – 15	10 – 11
	V_{15}	5	$\frac{2-1-2}{2(3)-(3)2}$	3 – 1 – (4)3 (80)* 2 – 1 – 3 (20)*	10 – 12	9 – 11
T. zwellendamensis	Z_5	5	$\frac{3(4)-1-3}{2-2}$	3 – 1 – 3	12 – 14	11 – 13

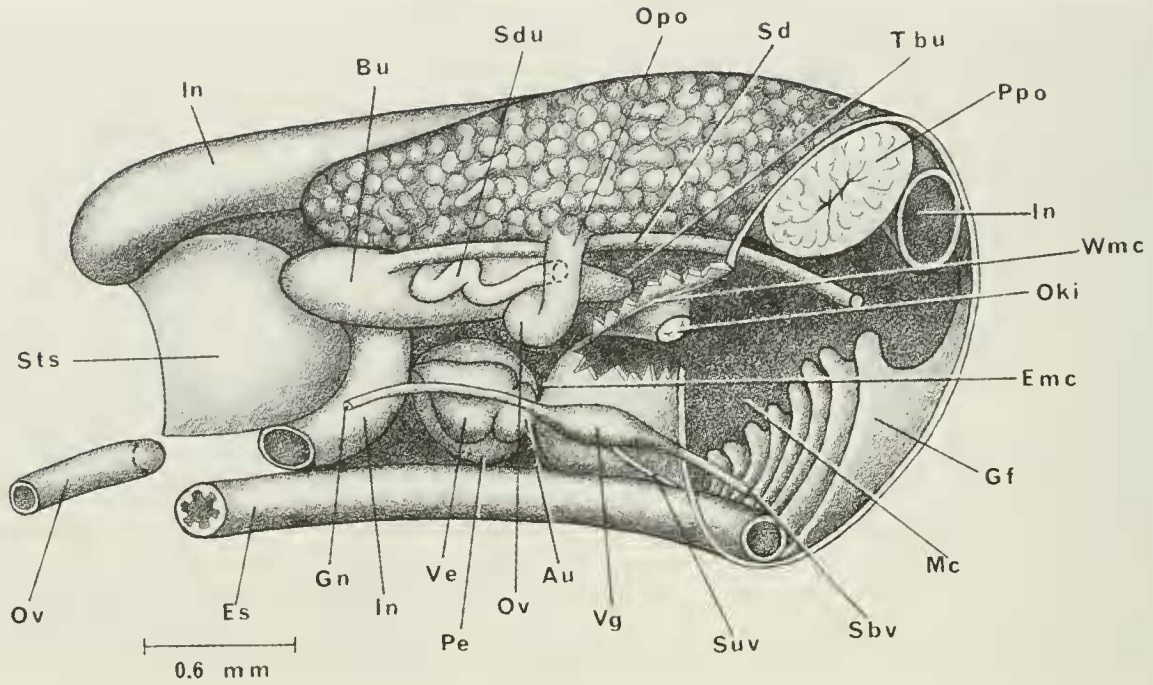

FIG. 18. Female *T. ventricosa* positioned exactly as in Fig. 17, but with the posterior stomach and digestive gland removed posteriorly (to the left) and a cut across the body through the mantle cavity, pallial oviduct and intestine (to the right) exposing the mantle cavity (Mc) and the structures within the cavity, e.g. opening of kidney through posterior wall of the mantle cavity (Oki), cross sections of the esophagus (Es), posterior pallial oviduct (Ppo), intestine (In), and spermathecal duct (Sd). The remaining gill filaments (Gf) of the ctenidium are seen.

The purpose of the illustration is to show the relationship of the elongate bursa copulatrix (Bu) to the posterior pallial oviduct (Pop), opening of the oviduct into the posterior pallial oviduct (Opo), and the anterior tip of the bursa (Tbu) within the cavity of the kidney in the funnel of the kidney leading to the opening of the kidney (Oki).

Au, auricle; Bu, bursa copulatrix; Emc, posterior end of the mantle cavity; Es, esophagus; Gf, gill filament; Gn, gonadal nerve; In, intestine; Mc, mantle cavity; Oki, opening of kidney into the posterior mantle cavity; Opo, opening of oviduct into posterior pallial oviduct; Ov, oviduct; Pe, pericardium; Ppo, posterior pallial oviduct; Sbv, subvisceral connective; Sd, spermathecal duct; Sdu, sperm duct; Sts, style sac; Suv, supra-visceral connective; Tbu, anterior tip of bursa copulatrix; Ve, ventricle; Vg, visceral ganglion; Wmc, reflected cut wall of mantle cavity.

TABLE 17. General cusp formula for each species of South African *Tomichia*. ( )* = % of cusps.

Taxon	Central tooth	Lateral tooth	Inner marginal	Outer marginal
T. differens	2(1) – 1 – (1)2 2(3) – (3)2	3 – 1 – 3(4)	9 – 13	9 – 11
T. natalensis	2 – 1 – 2 3 – 3	2(3) – 1 – 3	8 – 9	8 – 10
T. rogersi	2(3) – 1 – (3)2 2(3) – (3)2	2 – 1 – 3(4)	10 – 13	8 – 10
T. tristis	2 – 1 – 2 2 – 2	3 – 1 – (4)3 (66)* 3 – 1 – (2)3 (33)*	11 – 12	9 – 10
T. ventricosa	2 – 1 – 2 2(3) – (3)2	3(2) – 1 – 3(4)	10 – 15	8 – 11
T. zwellendamensis	3 – 1 – 3 2 – 2	3 – 1 – 3	12 – 14	11 – 13

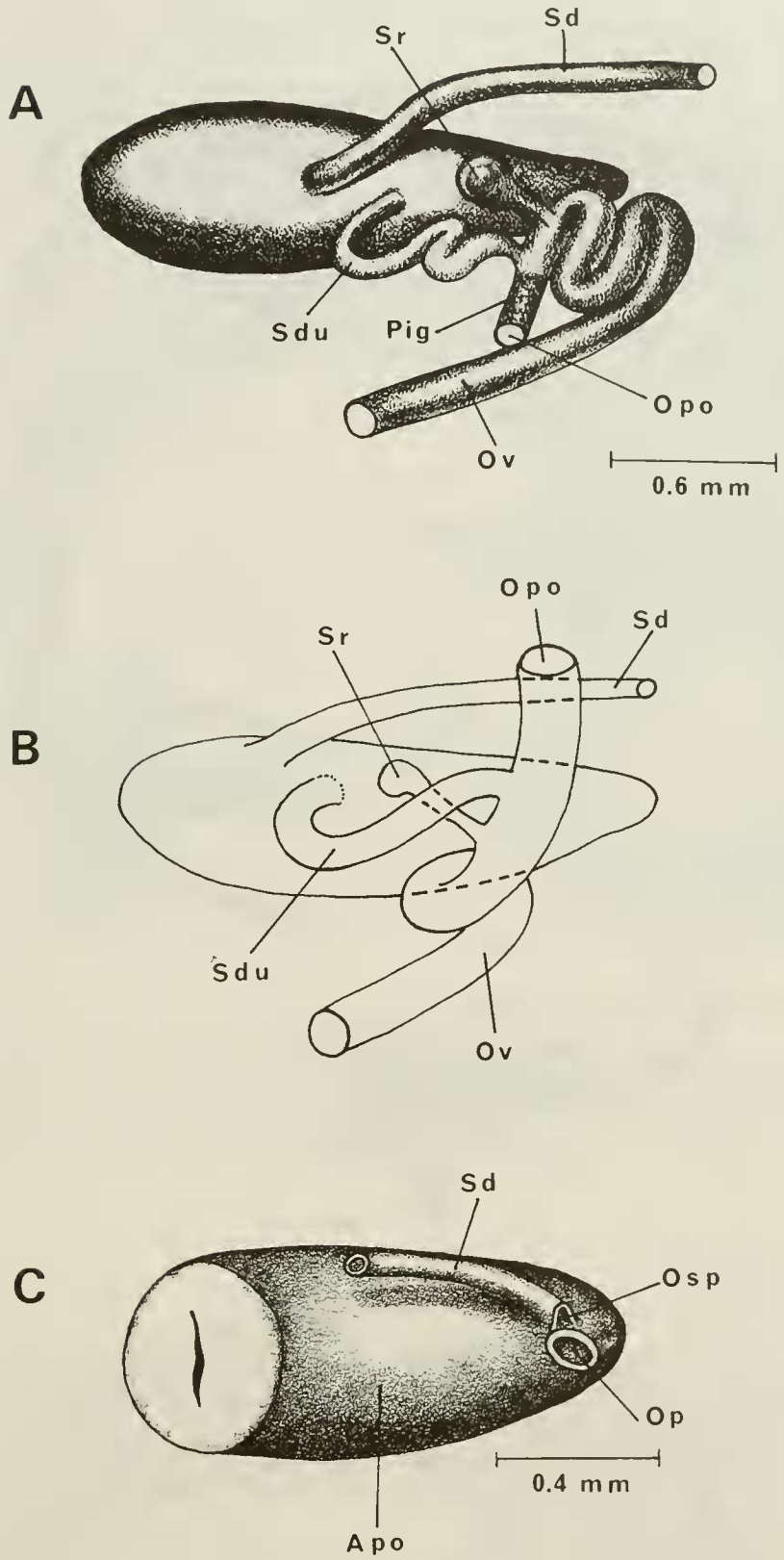

FIG. 19. Female reproductive system of *T. ventricosa*. A, B, bursa copulatrix complex with bursa positioned as in Figs. 17, 18. C, anterior end of pallial oviduct (Apo) showing the opening of the pallial oviduct (Op) at the end of a nipple-like extension of the pallial oviduct. The opening (Osp) of the spermathecal duct (Sd) is shown in relationship to the opening of the pallial oviduct.

In B, the positions of the ducts and organs are shown in usual configuration as in Fig. 18. In A, the oviduct at the pallial oviduct (Opo) has been shown pulled 90° towards the reader to show the seminal receptacle (Sr) in its usual position. Note the densely pigmented (Pig) section of the oviduct where it opens into the pallial oviduct.

Apo, anterior pallial oviduct; Op, anterior opening of pallial oviduct; Opo, opening of oviduct into the posterior pallial oviduct; Osp, anterior opening of spermathecal duct; Ov, oviduct; Pig, pigmented section of oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle.

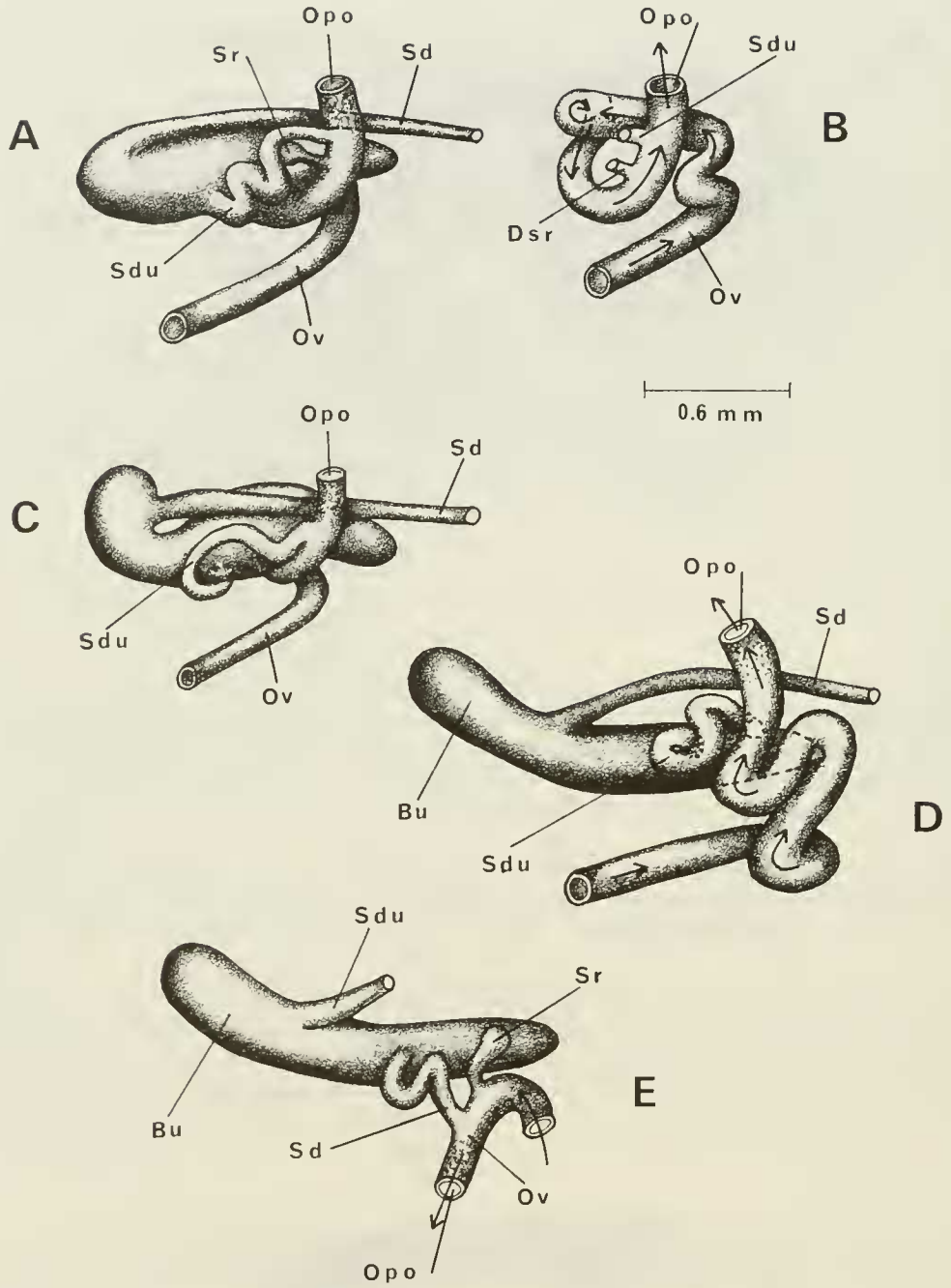

FIG. 20. Bursa copulatrix complex as in Fig. 19. A–C, *T. natalensis*; D, E, *T. rogersi*. The spermathecal duct enters the posterior bursa in *T. natalensis*. The posterior bursa is particularly elongate in *T. rogersi*. B, the coils of the oviduct and path of sperm are shown.

Bu, bursa copulatrix; Dsr, duct of seminal receptacle; Opo, opening of oviduct into posterior pallial oviduct; Ov, oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle.

nozzle-like extension at the anterior end of the pallial oviduct at the tip of which is the opening.

Male reproductive system (Figs. 21, 22)—The system is standard pomatiopsine. Penis with eversible papilla, ciliated anterior epithelium and glandular edge on proximal concave curvature (Fig. 22) The vas deferens does not have a thickened ejaculatory section either in the base of the penis or proximal to the base of the penis.

Nervous system—The nervous system is standard pomatiopsid. Measurements of neural structures are given in Table 14. The RPG ratio (Table 14) is 0.54, significantly larger than that in *Oncomelania* and *Pomatiopsis* and similar to that recorded for *Hydrobia* (Davis et al., 1976). This larger ratio is due to a comparatively long pleuro-supra-esophageal connective and indicates a more open (as opposed to condensed) central nervous system.

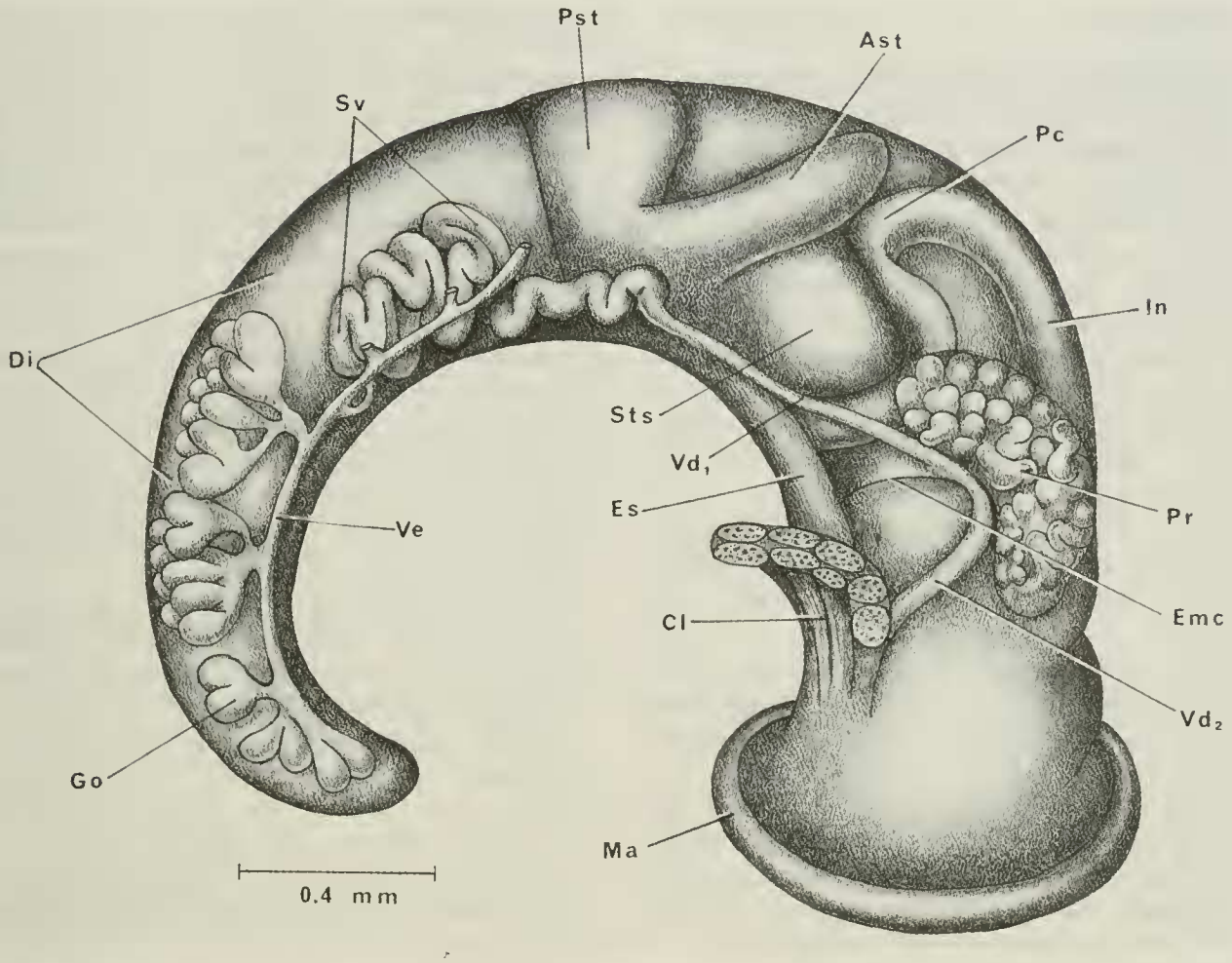

FIG. 21. Male reproductive system of *T. ventricosa*. Head and kidney tissue were removed. Part of the gonad (Go) was removed to reveal the coiled seminal vesicle (Sv).

Ast, anterior chamber of stomach; Cl, columellar muscle; Di, digestive gland; Emc, posterior end of the mantle cavity; Es, esophagus; Go, gonad; In, intestine; Ma, mantle edge = collar; Pc, pellet compressor; Pr, prostate; Pst, posterior chamber of stomach; Sts, style sac; Sv, seminal vesicle; Vd_1, vas deferens posterior to prostate; Vd_2, vas deferens anterior to prostate; Ve, vas efferens.

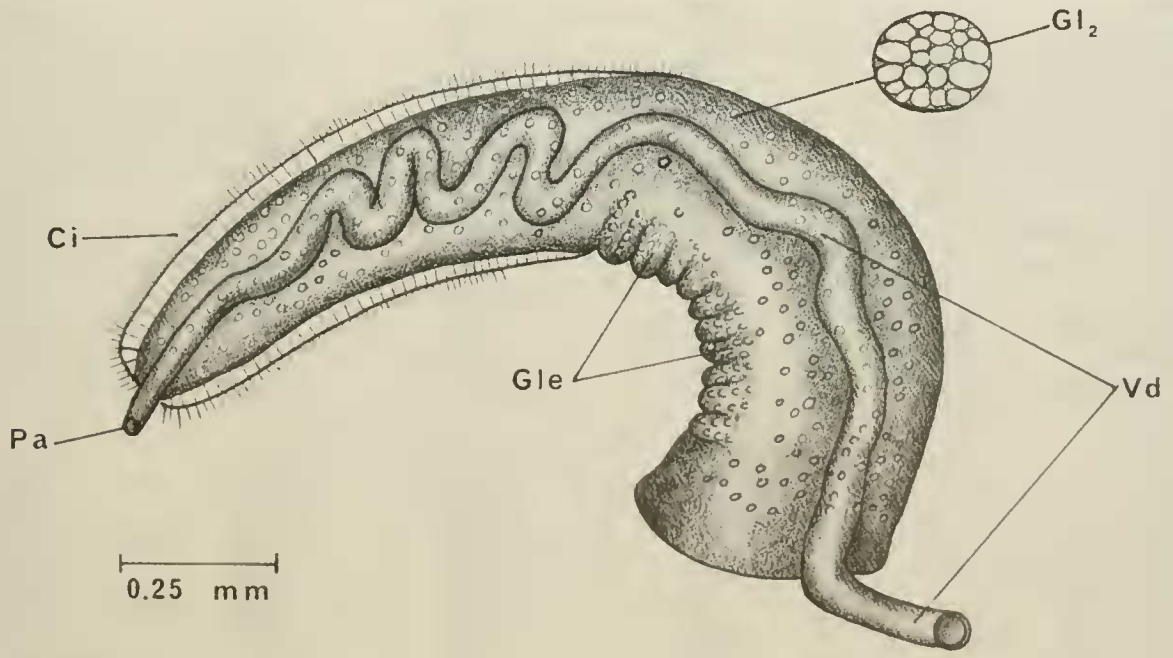

FIG. 22. Penis of *T. ventricosa*. Ci, cilia; Gle, glandular edge of the penis; Gl_2 subepithelial gland types; Pa, papilla; Vd, vas deferens.

T. differens

Shell (Fig. 8)—Type-locality (Appendix 1, D_1) not much eroded, males and females 6.0 to 6.5 whorls. Statistics in Table 12. Length of last three whorls 4.25 ± 0.14 mm (Fig. 12). Shape ovate (bullet-shaped). Whorls flat-sided to slightly convex, sutures shallow. Color light brown, glistening. Aperture ovate-pyriform with produced adapical end (Fig. 13), lips thick, peristome complete with thick parietal callus. Inner lip not reflected; abapical end of aperture projecting slightly below base of body whorl. Slight arc of columella seen inside aperture.

No umbilicus or only a chink(<5%). Smooth body and penultimate whorl (about 40%). Outer lip straight or with slight sinuation (side view).

Organ measurements—See Table 18 for measurements or ratios of non-neural organs; Table 19 for measurements of neural structures.

Unique features—The tip of the radular sac extends beyond the end of the buccal mass and curls dorsally between the cerebral nervous system and the buccal mass (Fig. 16B, Trs). Other aspects as in *T. ventricosa.*

Radula—See Fig. 9, Tables 15–17.

T. natalensis

Shell (Fig. 7)—Locality (N_3, Appendix 1), invariably entire with males 6.0 whorls and females 6.0 to 6.5 whorls. Statistics, Table 12. Length of last three whorls 4.10 ± 0.22 (Fig. 12). Shape ovate-conic. Whorls moderately convex, sutures correspondingly impressed. Color dark brown due to heavy periostracum. Peristome entire, with dark brown edge, thick. Aperture shape variable, widely ovate to subquadrate, slightly produced at adapical end in some specimens. Parietal callus well formed, straight to slightly sinuate. Inner lip not reflected over umbilical or basal areas of the body whorl. Inside aperture only very narrow strip of columella seen (Fig. 13).

No umbilicus; a few with chink. Shells smooth, dull, without pronounced growth lines, no spiral micro-lines. Outer lip of most shells with marked sinuation.

Organ measurements—See Table 20 for non-neural organs; Table 21 for neural structures.

Radula—See Fig. 9, Tables 15–17.

Unique features—The spermathecal duct enters the bursa at, or close to the posterior end of the latter (1) (Figs. 20A, C) and is separated from the opening of the sperm duct into

TABLE 18. Dimensions (mm) or number of non-neural organs of topotype *Tomichia differens,* D 77-13.

		No.	$\bar{X}$	Sd	Range
Organ (♀)					
Body	L.	5	8.32	0.36	8.0 –8.8
Buccal mass	L.	5	1.01	0.16	0.9 –1.3
Anterior pallial oviduct	L.	6	1.55	0.12	1.4 –1.7
Posterior pallial oviduct	L.	6	1.95	0.10	1.8 –2.1
Total pallial oviduct (Po)	L.	6	3.50	0.17	3.3 –3.8
Bursa copulatrix (Bc)	L.	6	1.11	0.11	1.0 –1.28
Bc/Po		6	0.31	0.04	0.26–0.37
Seminal receptacle	L.	3	0.14	0.03	0.10–0.16
Digestive gland	L.	5	3.32	0.22	3.0 –3.6
Gonad	L.	4	1.05	0.28	0.9 –1.1
Mantle cavity	L.	5	2.32	0.13	2.1 –2.4
Ctenidium	L.	4	1.82	0.27	1.6 –2.2
Gill filaments	No.	5	28.8	2.86	25–32
Organ (♂)					
Body	L.	5	8.92	0.76	8.0 –9.6
Prostate	L.	5	0.88	0.25	0.5 –1.20
Digestive gland	L.	4	4.88	0.83	4.0 –6.0
Gonad	L.	6	4.72	0.62	4.0 –5.4
Seminal vesicle	L.	4	1.40	0.28	1.0 –1.6
Penis	L.	5	1.94	0.38	1.5 –2.5
Mantle cavity	L.	5	2.22	0.15	2.0 –2.4
Ctenidium	L.	5	1.72	0.08	1.6 –1.8
Gill filaments	No.	5	27.6	2.60	26–32

the bursa by 0.26 mm or more, usually 0.30 mm. (2) In *T. ventricosa* this distance is usually 0.20 mm or less. (3) The opening of the sperm duct into the bursa is at the left ventro-lateral edge of the bursa or on the left dorso-lateral edge instead of mid-ventral bursa (Figs. 20A, C).

T. rogersi

Shell (Fig. 7)—Type-locality (Appendix 1, R_1). Mostly entire, males 7.0–7.5 whorls, females 6.5–7.0 whorls. Statistics in Table 12. Length of last three whorls 6.84 ± 0.18 mm (Fig. 12). Shape turreted. Whorls moderately

TABLE 19. Measurements (mm) of lengths of neural structures from female *Tomichia differens*.

Structure	No.	$\bar{X}$	Sd	Range
Cerebral ganglion	5	0.35	0.04	0.30–0.40
Cerebral commissure	5	0.22	0.06	0.16–0.30
Pleural ganglion—right (1)	5	0.16	0.01	0.14–0.16
—left	5	0.15	0.01	0.14–0.16
Pleuro-supraesophageal connective (2)	5	0.30	0.07	0.20–0.38
Supraesophageal ganglion (3)	5	0.15	0.02	0.14–0.18
Osphradiomantle nerve	5	0.16	0.06	0.10–0.20
Pleuro-subesophageal connective	5	0.03	0.03	0 –0.06
Subesophageal ganglion	5	0.14	0.03	0.10–0.16
Pedal ganglion	5	0.26	0.11	0.20–0.32
Pedal commissure	5	0.08	0.02	0.04–0.10
Statocyst (diameter)	3	0.11	0.01	0.10–0.12
Osphradial ganglion	7	0.42	0.06	0.32–0.48
Visceral ganglion	4	0.15	0.01	0.14–0.16
RPG ratio: 2/1 + 2 + 3	5	0.49	0.06	0.40–0.56

TABLE 20. Length dimensions (mm) or number of non-neural organs of *Tomichia natalensis*.

	No.	$\bar{X}$	Sd	Range
Organ (♀)				
Body	4	8.2	0.58	7.6 –8.7
Buccal mass	5	0.92	0.02	0.9 –0.94
Anterior pallial oviduct	3	1.53	0.15	1.4 –1.7
Posterior pallial oviduct	3	1.75	0.05	1.7 –1.8
Total pallial oviduct (Po)	4	3.18	0.10	3.1 –3.3
Bursa copulatrix (Bc)	5	1.26	0.06	1.2 –1.3
Bc/Po	4	0.40	0.02	0.38–0.42
Seminal receptacle	1	0.20	—	—
Digestive gland	4	3.45	0.24	3.2 –3.7
Gonad	3	1.20	0.17	1.0 –1.3
Mantle cavity	4	2.63	0.29	2.3 –3.0
Ctenidium	4	2.03	0.29	1.7 –2.4
Gill filaments	4	37.8	2.29	35–40
Organ (♂)				
Body	2	8.0	—	7.8 –8.2
Prostate	2	1.35	–	1.3 –1.4
Digestive gland	2	3.7	—	3.6 –3.8
Gonad	2	3.0	—	0
Seminal vesicle	2	1.1	—	0
Penis	3	2.77	0.55	2.4 –3.4
Mantle cavity	2	2.85	—	2.7 –3.0
Ctenidium	2	2.40	—	0
Gill filaments	2	30	—	0

convex, sutures correspondingly impressed. Color yellow brown, without heavy periostracum and surface thus glistening. Peristome complete, lips thickened but without dark brown edge. Aperture ovate, not produced at adapical end (Fig. 13); inner lip not reflected over umbilical or basal areas of the body whorl. Parietal callus well formed, straight or arcuate. Inside aperture columella not seen or only very narrow strip seen.

Umbilicus lacking, a chink, or moderately open. Shells smooth, without pronounced growth lines. Some shells have spiral microlines while others (<5%) have oddly spaced raised micro-cords that give area of the shell a malleated appearance. Outer lip of most shells straight or with very slight sinuation (side view).

Organ measurements—See Table 22 for non-neural organs; Table 23 for neural structures.

Radula—See Fig. 9, Tables 15–17.

Unique features—1) large size, 2) the bursa posterior to the opening of the spermathecal

TABLE 21. Measurements (mm) of lengths of neural structures from male *Tomichia natalensis*. N = 4.

Structure	$\bar{X}$	Sd	Range
Cerebral ganglion	0.22	0.02	0.30–0.24
Cerebral commissure	0.09	0.01	0.08–0.10
Pleural ganglion—right (1)	0.12	0.03	0.10–0.16
—left	0.22	0.08	0.16–0.34
Pleuro-supraesophageal connective (2)	0.36	0.03	0.34–0.40
Supraesophageal ganglion (3)	0.15	0.03	0.12–0.18
Osphradiomantle nerve	0.11	0.03	0.08–0.16
Pleuro-subesophageal connective	0.14	0.07	0.08–0.20
Pedal ganglion	0.21	0.01	0.02–0.22
Pedal commissure	0.09	0.01	0.08–0.10
Statocyst (diameter)	0.10	0.01	0.08–0.10
Osphradial ganglion (N = 3)	0.58	0.06	0.52–0.64
RPG ratio	0.57	0.04	0.52–0.61

TABLE 22. Length dimensions (mm) or number of non-neural organs of topotype *Tomichia rogersi*.

	No.	$\bar{X}$	Sd	Range
Organ (♀)				
Body	5	12.28	1.07	10.6 –13.4
Buccal mass	5	1.30	0.14	1.1 – 1.40
Anterior pallial oviduct	5	2.56	0.71	2.0 – 3.80
Posterior pallial oviduct	5	2.26	0.09	2.2 – 2.4
Total pallial oviduct (Po)	5	4.82	0.79	4.2 – 6.2
Bursa copulatrix (Bc)	5	1.70	0.11	1.6 – 1.8
Bc/Po	5	0.36	0.04	0.29– 0.40
Seminal receptacle	5	0.27	0.03	0.24– 0.30
Digestive gland	5	5.02	0.23	4.8 – 5.3
Gonad	5	2.26	0.33	2.0 – 2.8
Mantle cavity	5	4.16	0.09	4.0 – 4.2
Ctenidium	5	3.70	0.14	3.5 – 3.8
Gill filaments	5	51.6	2.70	50–55
Organ (♂)				
Body	5	12.58	0.78	11.9 –13.8
Prostate	5	1.28	0.11	1.20– 1.40
Digestive gland	5	6.84	0.32	6.34– 7.0
Gonad	5	7.24	0.43	7.0 – 8.0
Seminal vesicle	5	3.04	0.52	2.4 – 3.8
Penis	5	2.36	0.40	1.8 – 2.9
Mantle cavity	5	4.04	0.26	3.8 – 4.4
Ctenidium	5	3.46	0.26	3.2 – 3.8
Gill filaments	5	50.6	4.44	45–56

TABLE 23. Measurements (mm) of lengths of neural structures from female *Tomichia rogersi*.

Structure	No.	$\bar{X}$	Sd	Range
Cerebral ganglion	5	0.36	0.03	0.32–0.40
Cerebral commissure	5	0.27	0.03	0.24–0.30
Pleural ganglion—right (1)	5	0.18	0.02	0.16–0.20
—left	5	0.21	0.02	0.20–0.24
Pleuro-supraesophageal connective (2)	5	0.62	0.15	0.50–0.88
Supraesophageal ganglion (3)	5	0.20	0.02	0.18–0.22
Osphradiomantle nerve	3	0.18	0.03	0.14–0.20
Pleuro-subesophageal connective	5	0.08	0.11	0.02–0.28
Subesophageal ganglion	5	0.18	0.03	0.12–0.20
Pedal ganglion	5	0.30	0.03	0.26–0.34
Pedal commissure	5	0.08	0.04	0.02–0.10
Statocyst (diameter)	5	0.14	0.02	0.12–0.16
Osphradial ganglion	5	0.71	0.08	0.60–0.80
Visceral ganglion	4	0.25	0.02	0.22–0.26
RPG ratio: 2/1 + 2 + 3	5	0.61	0.06	0.57–0.71

TABLE 24. Measurements of individual shells of *Tomichia tristis* with entire whorls.

Whorl no.	Length	Width	Length of body whorl	Length of aperture	Width of aperture	Length of last three whorls
7.5	6.52	3.0	3.6	2.32	1.64	5.4
7.5	6.00	2.6	3.16	1.92	1.48	4.72
7.5	6.80	2.96	3.84	2.40	1.72	5.52
7.5	7.08	3.04	3.88	2.52	1.68	5.68
8.0	7.28	3.08	3.8	2.44	1.72	5.68

TABLE 25. Length dimensions (mm) or number of non-neural organs of *Tomichia tristis*.

	No.	$\bar{X}$	Sd	Range
Organ (♀)				
Body	4	12.63	1.82	11.3 –15.2
Buccal mass	3	1.3	0.10	1.2 – 1.4
Anterior pallial oviduct	4	2.0	0.33	1.6 – 2.4
Posterior pallial oviduct	4	2.53	0.49	1.8 – 2.8
Total pallial oviduct (Po)	4	4.53	0.28	4.2 – 4.8
Bursa copulatrix (Bc)	4	1.42	0.06	1.36– 1.50
Bc/Po	4	0.32	0.02	0.29– 0.35
Seminal receptacle	3	0.29	0.12	0.20– 0.42
Digestive gland	4	4.75	0.81	3.6 – 5.4
Gonad	3	1.97	0.21	1.8 – 2.2
Mantle cavity	4	3.95	0.41	3.4 – 4.4
Ctenidium	4	3.61	0.29	3.4 – 4.4
Gill filaments (no.)	4	56	2.94	52–59
Organ (♂)				
Body	2	11.1	—	10.6 –11.6
Prostate	1	1.2	—	—
Digestive gland	2	5.7	—	4.6 – 6.8
Gonad	1	4.8	—	—
Seminal vesicle	—	—	—	—
Penis	2	2.35	—	1.6 – 3.1
Mantle cavity	2	3.4	—	3.0 – 3.8
Ctenidium	2	3.0	—	2.6 – 3.4
Gill filaments (no.)	2	57.5	—	56–59

duct is frequently elongate, >0.70 mm (Figs. 20D, E); it is about 0.40 mm (and rarely attains 0.60) in *T. ventricosa*.

T. tristis

Shells (Fig. 7)—Various degrees of erosion of apical whorls. Mixed mature males and females with eroded apices measured 8.15 ± 0.67 mm length. Statistics, Tables 12, 24. Length of last three whorls 5.68 ± 0.29 mm (Fig. 12). Shape turreted. Whorls slightly convex to straight-sided. Sutures moderately shouldered. Color brown or dull yellow brown; periostracum moderate but sufficient to make shells dull. Peristome complete, lips moderately thickened, without dark brown edge. Aperture narrowly ovate, not produced adapically (Fig. 13). Inner lip slightly reflected over umbilical and basal areas of the body whorl. Parietal callus well formed, arcuate or straight, but sunk below the curvature of the body whorl. Inside aperture columellar strip prominent because of inner lip reflection.

TABLE 26. Measurements (mm) of lengths of neural structures from male and female *Tomichia tristis*. N = 4.

Structure	$\bar{X}$	Sd	Range
Cerebral ganglion	0.35	0.02	0.32–0.36
Cerebral commissure	0.26	0.04	0.20–0.30
Pleural ganglion—right (1)	0.19	0.02	0.16–0.20
—left	0.18	0.03	0.14–0.20
Pleuro-supraesophageal connective (2)	0.50	0.09	0.40–0.60
Supraesophageal ganglion (3)	0.18	0.03	0.14–0.20
Osphradiomantle nerve	0.13	0.03	0.10–0.16
Pleuro-subesophageal connective	0.13	0.15	0.02–0.34
Pedal ganglion (N = 2)	0.29	—	0.28–0.30
Statocyst (diameter) (N = 1)	0.10	—	—
Osphradial ganglion (N = 3)	0.77	0.18	0.60–0.96
Visceral ganglion	—	—	—
RPG ratio 2/1 + 2 + 3	0.61	0.09	0.50–0.72

TABLE 27. Length dimensions(mm) or number of non-neural organs of *Tomichia zwellendamensis*.

	No.	$\bar{X}$	Sd	Range
Organ (♀)				
Body	5	8.4	0.75	7.6 – 9.6
Buccal mass	3	0.88	0.19	0.74– 1.1
Anterior pallial oviduct	5	2.16	0.42	1.7 – 2.8
Posterior pallial oviduct	5	1.63	0.34	1.4 – 2.2
Total pallial oviduct (Po)	5	3.83	0.42	3.36– 4.20
Bursa copulatrix (Bc)	6	1.09	±0.23	0.80– 1.4
Bc/Po		0.29	0.04	0.23– 0.33
Seminal receptacle	3	0.19	0.02	0.16– 0.20
Digestive gland	6	3.07	0.30	2.6 – 3.4
Gonad	5	1.3	0.10	1.2 – 1.4
Mantle cavity	6	2.85	0.40	2.2 – 3.2
Ctenidium	6	2.57	0.41	1.96– 2.80
No. filaments	6	51.2	8.1	40–62
Organ (♂)				
Body	1	9.0	—	—
Prostate	2	1.07	—	1.01– 1.14
Digestive gland	1	4.8	—	—
Gonad	1	4.8	—	—
Seminal vesicle	2	1.0	—	—
Penis	2	1.5	—	1.3 – 1.7
Mantle cavity	1	2.8	—	—
Ctenidium	1	2.2	—	—
No. filaments	1	66	—	—

TABLE 28. Measurements (mm) of lengths of neural structures from male and female *Tomichia zwellendamensis*. N = 3.

Structure	$\bar{X}$	Sd	Range
Cerebral ganglion	0.26	0.02	0.24–0.28
Cerebral commissure	0.13	0.04	0.10–0.18
Pleural ganglion—right (1)	0.1	0	0
—left	0.11	0.02	0.09–1.2
Pleural-supraesophageal connective (2)	0.23	0.07	0.16–0.30
Supraesophageal ganglion (3)	0.11	0.01	0.08–0.10
Pleural-subesophageal connective	0.02	0.02	0 –0.02
Subesophageal ganglion (N = 2)	0.11	—	0.09–1.2
Pedal ganglion	0.20	0.02	0.18–0.22
Pedal commissure	0.03	0.03	0 –0.06
Statocyst (diameter)	0.09	0.01	0.08–0.10
Osphradial ganglion (N = 5)	0.47	0.09	0.34–0.56
Visceral ganglion	—	—	—
RPG ratio: 2/1 + 2 + 3	0.51	0.07	0.44–0.58

Shells with umbilical chink to wide open umbilicus. Shell surface rough, some shells with pronounced growth lines, many (60%) with malleation on the body whorl. Spiral micro-striations common. Outer lip sinuate (side view).

Organ measurements—See Table 25 for non-neural organs; Table 26 for neural structures.

Radula—See Fig. 10, Tables 15–17.

Unique features—none.

T. zwellendamensis

Shells (Fig. 8)—Locality (Appendix 1, Z_5), varying degress of erosion of apical whorls. Mature males and females 7.5 to 8.0 whorls. Statistics on shell measurements, Table 12. Length of last three whorls 4.06 ± 0.19 mm (Fig. 12). Shape, slender-turreted. Whorls moderately to quite convex; sutures deep. Color straw yellow. Periostracum slight, shells very fragile and translucent. Peristome not complete in >90%; if complete, only a hint of a parietal callus. Lips thin, without dark brown edge. Aperture ovate, not produced adapically (Fig. 13). Inner lip slightly reflected over umbilical and basal areas of the body whorl; slight arc of columella seen inside aperture because of this slight reflection.

Shells not umbilicate. Shell surface smooth, rarely with growth lines. Twist in columella evident in many shells where outer lip starts reflection. Outer lip straight (side view).

Organ measurements—See Table 27 for non-neural organs; Table 28 for neural structures.

Radula—See Fig. 10, Tables 15–17.

Unique features—only some shell character-states.

APPENDIX 3. Types examined and the status of *Tomichia cawstoni*

Types examined:

Hydrobia alabastrina Morelet, 1889: 19, pl. 2, fig. 5. British Museum (Nat. Hist.); examined 9 February 1978. Mixed lot; small specimen is *Rissoa capensis* Sowerby, 1892. Holotype as figured by Connolly, 1939.

Tomichia cawstoni Connolly, 1939: 585, text fig. 48L, British Museum (Nat. Hist.); examined 9 February 1978. The shell is yellow, straight and flat-sided, not umbilicate, very *Tricula*-like.

Tomichia differens Connolly, 1939: 583, text fig. 47M, South African Museum; examined circa 14 November 1977. Material indistinguishable from my collections at the type locality, D77-13, 19 November 1977.

Assiminea lirata Turton, 1932: pl. 35, fig. 1097. Zoological Museum, Oxford University; examined 10 February 1978. Holotype figured. This shell phenotype is the same seen in some individuals of a single population where other shells clearly resemble *Tomichia tristis,* described and figured by Morelet, 1889: 18, pl. 2, fig. 4, and Connolly, 1939.

Tomichia natalensis Connolly, 1939: 586, text fig. 470. British Museum (Nat. Hist.), examined 9 February 1978.

Tomichia producta Connolly, 1929: 242, pl. 14, fig. 40. British Museum (Nat. Hist.); examined 9 February 1978. Specimen clearly referable to *T. ventricosa*.

Hyrobia rogersi Connolly, 1929: 242, pl. 14, fig. 41. South African Museum; examined circa 14 November 1977.

Tomichia cawstoni was described from Kokstad, Cape Province. Kokstad is a small highland community situated N of national road R_2, to the east of the Transkei, close to the border of Natal Province. Dr. David Brown (now of the British Museum (Natural History)) and I have both searched for this species and have not located it. I examined stream banks, streams, and marshes around the area of Kokstad to no avail. There are very few streams in this region and Kokstad is situated in an isolated pocket in the hills.

A stream-marsh area along the main highway (R_2) opposite the turnoff to Kokstad appeared to provide a suitable habitat. This area, upon inspection, was polluted with oil. The fields surrounding were extensively used for grazing cattle. I presume this species to be extinct.